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THE NEST ARCHITECTURE OF STINGLESS BEES WITH SPECIAL REFERENCE TO THOSE OF COSTA RICA (Hymenoptera, Apidae)

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THE NEST ARCHITECTURE OF STINGLESS BEES WITH SPECIAL REFERENCE TO THOSE OF COSTA RICA (Hymenoptera, Apidae)

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With the present work, the University of Costa Rica initiates publications, as supplements, of studies too long to be included in the regular issues of the REVISTA DE BIOLOGIA TROPICAL.

This long–contemplated series fulfills the evident need of bringing to light special monographic studies on the flora, the fauna, the ecology, and other aspects of tropical biology. The need, equally evident, to make such studies readily aviable to Central American students and researchers of today and of the future, especially when dealing with the biota, phenomena or problems of our own area, has also been much on the minds of the directors of the Revista. This very interest explains the willingness to publish in these suplements works in languages other than Spanish, as has always been the norm of the Revista de Biología Tropical.

The comprehensive study of the nest architecture of stingless bees, the first of our supplements, is the result of sustained cooperation between a distinguished entomologist from the University of Kansas and another from the University of Costa Rica, and is a good omen as to the quality of those to follow.

Con la presente obra inicia la Universidad de Costa Rica la publicación en forma de suplementos de la REVISTA DE BIOLOGIA TROPICAL de trabajos de extensión excesiva para la inclusión en los fascículos ordinarios que la componen. Constituye esto la realización de un propósito abrigado desde hace muchos años, ya que se hacía evidente la necesidad de un instrumento para la publicación de estudios monográficos de la fauna, la flora, la ecología, u otros aspectos de la biología del trópico. Coincidía esta necesidad con el interés que los directores de la Revista comparten con sus colegas istmeños por canalizar hacia la prensa científica de la región los estudios de los especialistas de todo el mundo sobre biota o problemas biológicos del área centroamericana y así hacerlos fácilmente asequibles a nuestros investigadores y estudiantes de hoy y del futuro. Este mismo interés explicaría por sí solo la disposición de publicar en estos suplementos trabajos en idiomas distintos del español, lo cual ha sido también la norma de la Revista de Biología Tropical.

El interesantísimo estudio de la arquitectura de los nidos de las abejas melipónidas con que se inicia esta serie de suplementos, producto de la cooperación de un entomólogo distinguido de la Universidad de Kansas y de otro de la Universidad de Costa Rica, es en sí un buen augurio para los que hayan de seguirlos.

The purpose of this work is to provide comparative information on the nest sites and architecture of the whole apid tribe Meliponini as well as data on the hitherto undescribed nests of certain species from Costa Rica. The field work involved opening limited numbers of nests of as many species as possible and recording the nest structure and organization by means of notes, diagrams, and photographs. We have not attempted the detailed kind of examination of architecture such as **Nogueira–Neto's** (40) study of cells, for such investigations are best done with colonies in hives. Our interest has been in the field conditions and architectural adaptations to various kinds of cavities.

The stingless bees are the most common bees and possibly the most important pollinators in the American tropics. They are less numerous in the African, Asiatic and Australian tropics but nonetheless are a significant element of the fauna, especially in the Malayan area. They are also sources of minor quantities of honey and wax. In addition to their major positive value as pollinators, some of them are significant pests. Various species cut leaves, buds, and bark of young trees, causing significant losses to agriculture and horticulture, and transmit certain plant diseases.

Table I. Names of Meliponini whose nests are discussed. In the first column, the generic names *(Trigona, Dactylurina, Lestrimelitta, Meliponula,* and *Melipona)* are in capitals and also abbreviated with each species; subgenera are shown by secondary headings.

Name accepted in present paper	Combination based on Moure (34)	Well known specific synonym
TRIGONA		
Meliplebeia		
1. *T. beccarii* Gribodo	*Meliplebeia beccarii*	
2. *T. d. denoiti* Vachal	*Plebeina denoiti*	
3. *T. lendliana* Friese	*Plebeiella lendliana*	
4. *T. nebulata abrassarti* Cockerell	*Apotrigona nebulata abrassarti*	
5. *T. nebulata komiensis* Cockerell	*Apotrigona nebulata komiensis*	
6. *T. tanganyikae medionigra* Cockerell	*Meliplebeia tanganyika medionigra*	
Plebeia		
7. *T. australis* Friese	*Austroplebeia australis*	*cassiae* Cockerell
8. *T. cincta* Mocsary	*Austroplebeia cincta*	
9. *T. domiciliorum* Schwarz[1]	*Plebeia (Plebeia) domiciliorum*	
10. *T. droryana* Friese	*Plebeia (Plebeia) droryana*	
11. *T. emerina* Friese	*Plebeia (Plebeia) emerina*	
12. *T. frontalis* Friese	*Plebeia (Plebeia) frontalis*	
13. *T. minima* Gribodo	*Plebeia (Plebeia) minima*	*goeldiana* Friese
14. *T. molesta* (Puls)	*Plebeia (Plebeia) molesta*	
15. *T. mosquito* Smith	*Plebeia (Plebeia) mosquito*	

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[1] *T. domiciliorum* is a synonym of *T. franki* Friese according to Moure (personal communication).

16. *T. quadripunctata bipartita* (Lepeletier)		
17. *T. q. quadripunctata* (Lepeletier)	*Plebeia (Schwarziana) quadripunctata bipartata*	
	Plebeia (Schwarziana) q. quadripunctata	
18. *T.* sp. A	*Plebeia (Plebeia)* sp. A	
19. *T. remota* Holmberg	*Plebeia (Plebeia) remota*	
20. *T. schrottkyi* Friese	*Plebeia (Friesella) schrottkyi*	
21. *T. tica* Wille	*Plebeia (Plebeia) tica*	

Nogueirapis

22. *T. mirandula* Cockerell	*Partamona (Nogueirapis) mirandula*	

Axestotrigona

23. *T. eburnensis* Darchen	*Axestotrigona eburnensis*	
24. *T. sawadogoi* Darchen	*Axestotrigona sawadogoi*	
25. *T. togoensis* Stadelmann	*Axestotrigona togoensis*	

Hypotrigona

26. *T. araujoi* Michener	*Hypotrigona (Hypotrigona) araujoi*	*gribodoi* form "landula" (44)
27. *T. braunsi* Kohl	*Hypotrigona (Hypotrigona) braunsi*	*gribodoi* and form "cassuso" (1, 44)
28. *T. gribodoi* Magretti	*Hypotrigona (Hypotrigona) gribodoi*	

Trigonisca

29. *T. atomaria* Cockerell	*Hypotrigona (Trigonisca) atomaria*	
30. *T. buyssoni* Friese	*Hypotrigona (Trigonisca) buyssoni*	
31. *T. duckei* Friese	*Hypotrigona (Trigonisca) duckei*	
32. *T. goeldiana* Friese	*Hypotrigona (Trigonisca) goeldiana*	
33. *T. muelleri* Friese	*Hypotrigona (Leurotrigona) muelleri*	
34. *T. sp. B*	*Hypotrigona (Trigonisca) sp. B*	

Scaura

35. *T. latitarsis* Friese	*Scaura (Scaura) latitarsis*	
36. *T. longula* (Lepeletier)	*Scaura (Scaura) longula*	
37. *T. tenuis* (Ducke)	*Scaura (Scaura) tenuis*	
38. *T. timida* Silvestri	*Scaura (Schwarzula) timida*	

Partamona

39. *T. cupira* Smith	*Partamona (Partamona) cupira*	*testacea* subsp. (30, 63)
40. *T. sakagamii* Moure MS	*Partamona (Partamona) sakagamii*	
41. *T. testacea helleri* Friese	*Partamona (Partamona) testacea helleri*	
42. *T. testacea musarum* Cockerell	*Partamona (Partamona) testacea musarum*	
43. *T. testacea orizabaensis* Strand	*Partamona (Partamona) testacea orizabensis*	
44. *T. t. testacea* Klug	*Partamona (Partamona) t. testacea*	

Paratrigona

45. *T. guatemalensis* Schwarz	*Partamona (Paratrigona) guatemalensis*	
46. *T. impunctata* (Ducke)	*Partamona (Aparatrigona) impunctata*	
47. *T. isopterophila* Schwarz	*Partamona (Aparatrigona) isopteraphila*	
48. *T. lineata nuda* Schwarz	*Partamona (Paratrigona) lineata nuda*	
49. *T. ornaticeps* Schwarz	*Partamona (Paratrigona) ornaticeps*	
50. *T. peltata pacifica* Schwarz	*Partamona (Paratrigona) peltata pacifica*	
51. *T. p. peltata* Spinola	*Partamona (Paratrigona) p. peltata*	*o. opaca* of Schwarz (part)
52. *T. subnuda* Moure	*Partamona (Paratrigona) subnuda*	*petropolis* Schwarz

Scaptotrigona

53. *T. bipunctata* (Lepeletier) or *postica* Latreille	*Nannotrigona (Scaptotrigona) bipunctata*	
54. *T. iheringi* (Ducke)	*Nannotrigona (Scaptotrigona) iheringi*	
55. *T. mexicana subobscuripennis* Schwarz	*Nannotrigona (Scaptotrigona) mexicana subobscuripennis*	

56. *T. pachysoma* Cockerell	*Nannotrigona (Scaptotrigona) pachysoma*	
57. *T. pectoralis* Dalla Torre	*Nannotrigona (Scaptotrigona) pectoralis*	
58. *T. postica* Latreille	*Nannotrigona (Scaptotrigona) postica*	
59. *T. tubiba* Smith	*Nannotrigona (Scaptotrigona) tubiba*	
60. *T. xanthotricha* Moure	*Nannotrigona (Scaptotrigona) xanthotricha*	

Nannotrigona

61. *T. mellaria* Smith	*Nannotrigona (Nannotrigona) mellaria*
62. *T. testaceicornis perilampoides* Cresson	*Nannotrigona (Nannotrigona) testaceicornis perilampoides*

Cephalotrigona

63. *T. c. capitata* Smith	*Cephalotrigona c. capitata*
64. *T. capitata zexmeniae* Cockerell	*Cephalotrigona capitata zexmeniae*
65. *T. femorata* Smith	*Cephalotrigona femorata*

Oxytrigona

66. *T. obscura* Friese	*Oxytrigona obscura*
67. *T. tataira mellicolor* Packard	*Oxytrigona tataira mellicolor*
68. *T. t. tataira* Smith	*Oxytrigona t. tataira*

Tetragona

69. *T. a. apicalis* Smith	*Tetragonilla a. apicalis*	
70. *T. atripes collina* Smith	*Tetragonilla atripes collina*	
71. *T. buchwaldi* Friese	*Trigona (Tegragonisca) buchwaldi*	
72. *T. carbonaria* Smith	*Trigona (Tetragonula) carbonaria*	
73. *T. clavipes* (Fabricius)	*Trigona (Tetragona) clavipes*	
74. *T. clypearis* Friese	*Trigona (Tetragonula) clypearis*	*wybenica* Cockerell
75. *T. dorsalis* Smith	*Trigona (Tetragona) dorsalis*	

76. *T. flavicornis* (Fabricius)	*Trigona (Frieseomelitta) flavicornis*	
77. *T. freiremaiai* Moure	*Trigona (Frieseomelitta) freiremaiai*	
78. *T. f. fuscobalteata* Cameron	*Tetragonula f. fuscobalteata*	
79. *T. fuscobalteata pagdeni* Schwarz	*Tetragonula fuscobalteata pagdeni*	
80. *T. genalis* Friese	genus (?)[1] *genalis*	
81. *T. ghilianii* (Spinola)	*Trigona (Duckeola) ghilianii*	
82. *T. hockingsi* Cockerell	*Trigona (Tetragonula) hockingsi*	
83. *T. iridipennis* Smith	*Trigona (Tegragonula) iridipennis*	
84. *T. itama* Cockerell	*Heterotrigona itama*	
85. *T. j. jaty* Smith	*Trigona (Tetragonisca) j. jaty*	
86. *T. javanica* Gribodo	*Lepidotrigona javanica*	
87. *T. leucogastra chiriquiensis* Schwarz	*Trigona (Geotrigona) leucogastra chiriquiensis*	
88. *T. lurida* Smith	*Trigona (Ptilotrigona) lurida*	*heideri* Friese
89. *T. monbuca* Smith	*Trigona (Geotrigona) mombuca*	
90. *T. nigra paupera* (Provancher)	*Trigona (Frieseomelitta) nigra paupera*	
91. *T. perangulata* Cockerell	*Trigona (Tetragona) perangulata*	
92. *T. portoi* Friese	*Trigona (Frieseomelitta) portoi*	
93. *T. sarawakensis* Schwarz	*Tetragonula sarawakensis*	
94. *T. silvestrii* Friese	*Trigona (Frieseomelitta) silvestrii*	
95. *T. smithii* Bingham	*Trigona (Tetragonula) smithii*	
96. *T. terminata* Smith	*Lepidotrigona terminata*	
97. *T. varia* (Lepeletier)	*Trigona (Frieseomelitta) varia*	

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[1] This species was not listed by Moure and appears not to fit in his classification.

Trigona s. str.

98. *T. amalthea* (Olivier)	*Trigona (Trigona) amalthea*	*trinidadensis* of Schwarz (63)
99. *T. chanchamayoensis* Schwarz	*Trigona (Trigona) chanchamayoensis*	
100. *T. c. cilipes* (Fabricius)	*Trigona (Trigona) c. cilipes*	*compressa* Latreille

101. *T. corvina* Cockerell	*Trigona (Trigona) corvina*	
102. *T. crassipes* (Fabricius)	*Trigona (Trigona) crassipes*	
103. *T. dallatorreana* Friese	*Trigona (Trigona) dallatorreana*	
104. *T. d. dimidiata* Smith	*Trigona (Trigona) d. dimidiata*	
105. *T. f. fulviventris* Guérin	*Trigona (Trigona) f. fulviventris*	
106. *T. fulviventris guianae* Cockerell	*Trigona (Trigona) fulviventris guianae*	
107. *T. fuscipennis* Friese	*Trigona (Trigona) fuscipennis*	*amalthea* of Schwarz (63)
108. *T. hyalinata branneri* Cockerell	*Trigona (Trigona) hyalinata branneri*	
109. *T. h. hyalinata* (Lepeletier)	*Trigona (Trigona) h. hyalinata*	
110. *T. hypogea* Silvestri	*Trigona (Trigona) hypogea*	
111. *T. nigerrima* Cresson	*Trigona (Trigona) nigerrima*	
112. *T. p pallens* (Fabricius)	*Trigona (Trigona) p. pallens*	*pallida* Latreille
113. *T. recursa* Smith	*Trigona (Trigona) recursa*	
114. *T. silvestriana* Vachal	*Trigona (Trigona) silvestriana*	
115. *T. spinipes* (Fabricius)	*Trigona (Trigona) spinipes*	*ruficrus* Latreille

DACTYLURINA

116. *D. staudingeri* Gribodo	*Dactylurina staudingeri*

LESTRIMELITTA

Cleptotrigona

117. *L. cubiceps* Friese	*Lestrimelitta (Cleptotrigona) cubiceps*

Lestrimelitta s. str.

118. *L. ehrhardti* Friese	*Lestimelitta (Lestrimelitta) ehrhardti*
119. *L. limao* Smith	*Lestrimelitta (Lestrimelitta) limao*

MELIPONULA

120. *M. bocandei* (Spinola)	*Meliponula bocandei*	

MELIPONA

121. *M. anthidioides* Lepeletier	*Melipona anthidioides*	
122. *M. b. beecheii* Bennett	*Melipona b. beecheii*	
123. *M. compressipes manaosensis* Schwarz	*Melipona compressipes manaosensis*	
124. *M. f. fasciata* Latreille	*Melipona f. fasciata*	
125. *M. fasciata melanopleura* Cockerell	*Melipona fasciata melanopleura*	
126. *M. f. favosa* (Fabricius)	*Melipona f. favosa*	
127. *M. favosa phenax* Cockerell	*Melipona favosa phenax*	
128. *M. flavipennis* Smith	*Melipona flavipennis*	
129. *M. fuscata melanoventer* Schwarz	*Melipona fuscata melanoventer*	
130. *M. interrupta grandis* Guérin	*Melipona interrupta grandis*	
131. *M. interrupta triplaridis* Cockerell	*Melipona interrupta triplaridis*	
132. *M. marginata amazonica* Schulz	*Melipona marginata amazonica*	
133. *M. marginata carrikeri* Cockerell	*Melipona marginata carrikeri*	
134. *M. m. marginata* Lepeletier	*Melipona m. marginata*	
135. *M. n. nigra* Lepeletier	*Melipona n. nigra*	*schencki picadensis* Strand
136. *M. nigra schencki* Gribodo	*Melipona nigra schencki*	
137. *M. p. pseudocentris* Cockerell	*Melipona p. pseudocentris*	
138. *M. quadrifasciata* Lepeletier	*Melipona quadrifasciata*	
139. *M. quinquefasciata* Lepeletier	*Melipona quinquefasciata*	
140. *M. rufiventris* Lepeletier	*Melipona rufiventris*	
141. *M. santhilarii* Lepeletier	*Melipona santhilarii*	
142. *M. scutellaris* Latreille	*Melipona scutellaris*	
143. *M. seminigra abunensis* Cockerell	*Melipona seminigra abunensis*	
144. *M. seminigra merrillae* Cockerell	*Melipona seminigra merrillae*	

UNPLACED

145. *T. turusiri* Janvier	? *turusiri*	

CLASSIFICATION AND NOMENCLATURE

At least meager information on nests has been obtained for 145 kinds of stingless bees. In some cases this is little more than the nest location and usually also the appearance of the entrance. In other cases detailed information is available. Table 1 lists the species concerned, showing the classification that we prefer and also that of Padre J.S. Moure. The difference between these classifications is more in the degree of splitting of various groups than in the relationships indicated by the classifications, but the resulting nomenclatural differences are unfortunate. We believe that fewer, larger groups (genera) are usually more useful than more and smaller ones.

There are a few points where differences in relationships are indicated in the classifications. Examples are as follows: *Nogueirapis* differs from *Plebeia* in only one group character and probably should be included in *Plebeia*; it seems to us only distantly related to *Partamona*. The close relations of *Nannotrigona* to *Scaptotrigona* suggested by Moure's classification seem doubtful to us. Unfortunately several long–established specific names in the group have been changed in recent years for various reasons. Such changes are also shown in Table 1.

The number of references to stingless bee nests is large. We have not attempted to make the list of references on meliponine nests complete in this paper but have referred to the most recent or comprehensive pertinent treatments for each species and to the older references when they contain more details. Older and sometimes historically interesting references can be found in the publications cited. Some general treatments are those of **Kerr** and **Laidlaw** (25), **Michener** (33), **Moure, Nogueira–Neto** and **Kerr** (36), **Nogueira–Neto** (41), and **Schwarz** (63).

NEST LOCATIONS

A.— General Account. Most meliponine nests are found in cavities which the bees appropriate, often reduce in size for their own purposes, and otherwise modify, but which they do not dig, if the substrate is solid soil or wood. They probably do, sometimes, enlarge or make their own cavities in termite or ant nests. Some species construct their nests in partially or fully exposed situations. Table 2 lists typical locations for each species. It should be noted, however, that most species can occupy nontypical situations when the opportunity arises; the table, therefore, does not give a complete account of all the strange sites that may occasionally be occupied. For example, a nest of *Melipona quadrifasciata* has been found in the mud nest of an oven bird, *Furnarius* (**Moure, Nogueira–Neto** and **Kerr**, 36) although the species typically nests elsewhere, as shown in the table.

Colonies of stingless bees range in population from a few hundred to many thousands and the worker bees themselves from 2 to 13.5 mm in length. It is therefore not surprising that some colonies occupy little space, e.g., a tubular hollow 36 cm long by 1.6 cm in diameter in a liana or aerial root (*Trigonisca*) while others occupy large spaces, e.g., 130 x 20 cm. in a hollow trunk or an ovoid 50 x 85 cm in the case of an exposed nest. Some species of stingless bees consistently live in cavities that are well insulated and presumably subject to little

TABLE 2

NEST SITES[1]

Species and references CR = treated in the section on Costa Rican nests	1. In ground	2. Among roots at foot of tree	3. Tree cavities	4. Slender tubular tree cavities	5. Planiform cavities	6. Artificial cavities	7. In termite nests	8. In ant nests	9. Partly exposed	10. Exposed
TRIGONA										
Meliplebeia										
1. *T. beccarii* (11, 43, 67, 68)	++									
2. *T. d. denoiti*, etc. (67, 68)							Gn			
3. *T. lendliana* (46)	++									
4. *T. nebulata abrassarti* (11)	++									
5. *T. nebulata komiensis* (6, 11)							G, Ec			
6. *T. tanganyikae medionigra* (46)	++									
Plebeia										
7. *T. australis* (32)			++	++						
8. *T. cincta* (32)			++							
9. *T. domiciliorum* (47)						++				
10. *T. droryana* (18, 21, 29)			++			++				
11. *T. emerina* (18, 21, 36, 56, 63)			++	++		++				

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[1] The symbol ++ indicates a common or the only known site, + indicates an uncommon site. In columns 7 and 8, when details are known, we have used other symbols as follows: G, nest in ground; E, nest (of ant or termite) exposed; T, nest in tree cavity; c, bees occupy cavity made in termite nest by other animals, e.g., birds, n, bees ocupy natural cavity in termite nest; b, bees apparently make their own cavity in ant or termite nest.

Table 2 (cont.)

Species and references CR = treated in the section on Costa Rican nest	1. In ground	2. Among roots at foot of tree	3. Tree cavities	4. Slender tubular tree cavities	5. Planiform cavities	6. Artificial cavities	7. In termite nests	8. In ant nests	9. Partly exposed	10. Exposed
12. *T. frontalis* (C. R.)			++	++						
13. *T. minima* (4, 29, 63)				++		++				
14. *T. molesta* (63)			++							
15. *T. mosquito* (29)			+			++				
16. *T. quadripunctata bipartita* (18, 21, 63)	++									
17. *T. q. quadripunctata* (18, 21, 29, 63)	++									
18. *T. sp. A* (C.R.)			++							
19. *T. remota* (36)			++			++				
20. *T. schrottkyi* (18, 21, 29, 36, 63)			++			++				
21. *T. tica* (75)				++						
Nogueirapis										
22. *T. mirandula* (72, 74)	++									
Axestotrigona										
23. *T. eburnensis* (12)							E			

Table 2 (cont.)

II – 3

Species and references CR = treated in the section on Costa Rican nests	1. In ground	2. Among roots at foot of tree	3. Tree cavities	4. Slender tubular tree cavities	5. Planiform cavities	6. Artificial cavities	7. In termite nests	8. In ant nests	9. Partly exposed	10. Exposed
24. *T. sawadogoi* (12)							E			
25. *T. togoensis* (15, 44, 67, 68)			++							
Hypotrigona										
26. *T. araujoi* (31, 44)				++						
27. *T. braunsi* (1, 31, 44)				++		++			++	
28. *T. gribodoi* (43)				++	++					
Trigonisca										
29. *T. atomaria* (C. R.)				++						
30. *T. buyssoni* (C. R.)				++						
31. *T. duckei* (C. R.)				++						
32. *T. goeldiana* (29)				++						
33. *T. muelleri* (19, 63)				++						
34. *T. sp. B* (C.R.)				++						

Table 2 (cont.)

Species and references CR = treated in the section on Costa Rican nests	1. In ground	2. Among roots at foot of tree	3. Tree cavities	4. Slender tubular tree cavities	5. Planiform cavities	6. Artificial cavities	7. In termite nests	8. In ant nests	9. Partly exposed	10. Exposed
Scaura										
35. *T. latitarsis* (C.R., 59,63,65)							Eb			
36. *T. longula* (63)			++				G			
37. *T. tenuis* (26)						++				
38. *T. timida* (65)			++							
Partamona										
39. *T. cupira* (C.R., 18, 21, 63)	+		+			++			++	+
40. *T. sakagamii* (26)			++							
41. *T. testacea helleri* (18, 21)									++	
42. *T. testacea musarum* (C. R.)										++
43. *T. testacea orizabensis* (48)						++			++	
44. *T. t. testacea* (9, 26)	++									
Paratrigona										
45. *T. guatemalensis* (C. R.)										++
46. *T. impunctata* (63)							++			

Table 2 (cont.)

II – 5

Species and references CR = treated in the section on Costa Rican nests	1. In ground	2. Among roots at foot of tree	3. Tree cavities	4. Slender tubular tree cavities	5. Planiform cavities	6. Artificial cavities	7. In termite nests	8. In ant nests	9. Partly exposed	10. Exposed
47. *T. isopterophila* (63)							E			
48. *T. lineata nuda* (62, 63)	++									
49. *T. ornaticeps* (C. R.)			++							
50. *T. peltata pacifica* (63)										++
51. *T. p. peltata* (C. R., 63)								Eb	++	++
52. *T. subnuda* (18, 21, 63)	++									
Scaptotrigona										
53. *T. bipunctata* or *postica* (3, 20)			++							
54. *T. iheringi* (18, 21)			++							
55. *T. mexicana suboscuripennis* (C. R.)			++							
56. *T. pachysoma* (30)			++			++				
57. *T. pectoralis* (C. R.)			++							
58. *T. postica* (63)			++							
59. *T. tubiba* (18, 21, 29, 36, 63)			++							
60. *T. xanthotricha* (9)			++							

Table 2 (cont.)

Species and references CR = treated in the section on Costa Rican nests	1. In ground	2. Among roots at foot of tree	3. Tree cavities	4. Slender tubular tree cavities	5. Planiform cavities	6. Artificial cavities	7. In termite nests	8. In ant nests	9. Partly exposed	10. Exposed
Nannotrigona										
61. *T. mellaria* (C. R.)			++							
62. *T. testaceicornis perilampoides* (C.R., 30)			++			++				
Cephalotrigona										
63. *T. c. capitata* (18,21,29,63)	++		++							
64. *T. capitata zexmeniae* (C. R., 63)			++							
65. *T. femorata* (26)			++							
Oxytrigona										
66. *T. obscura* (9)			++							
67. *T. tataira mellicolor* (C. R.)			++							
68. *T. t. tataira*, etc. (63)			++							
Tetragona										
69. *T. a. apicalis* (77)			++							
70. *T. atripes collina* (77)		++								
71. *T. buchwaldi* (74)	++									

Table 2 (cont.)

Species and references CR = treated in the section on Costa Rican nests	1. In ground	2. Among roots at foot of tree	3. Tree cavities	4. Slender tubular tree cavities	5. Planiform cavities	6. Artificial cavities	7. In termite nests	8. In ant nests	9. Partly exposed	10. Exposed
72. *T. carbonaria* (32)			++							
73. *T. clavipes* (3, 5, 18, 21, 29, 52, 66)	+	++	++							
74. *T. clypearis* (32)					++					
75. *T. dorsalis* (C.R.,10, 26, 30, 47)		++	++							
76. *T. flavicornis* (26)			++							
77. *T. freiremaiai* (35)			++							
78. *T. f. fuscobalteata* (77)						++				
79. *T. fuscobalteata pagdeni* (77)						++				
80. *T. genalis* (32)			++							
81. *T. ghilianii* (26)				++						
82. *T. hockingsi* (32)			++							
83. *T. iridipennis* (32, 57, 58, 60, 63)	+	+	++	+	+	++	+			
85. *T. i. jaty* (C.R.,63)	+		++	++		++				
86. *T. javanica* (60)			++							
87. *T. leucogastra chiriquiensis* (C. R.)	++									
88. *T. lurida* (9)		++								

Table 2 (cont.)

Species and references CR = treated in the section on Costa Rican nests	1. In ground	2. Among roots at foot of tree	3. Tree cavities	4. Slender tubular tree cavities	5. Planiform cavities	6. Artificial cavities	7. In termite nests	8. In ant nests	9. Partly exposed	10. Exposed
89. *T. mombuca* (18, 21, 29, 42)	++									
90. *T. nigra paupera* (C. R., 30, 54)			++			++				
91. *T. perangulata* (C. R.)			++							
92. *T. portoi* (26)				++						
93. *T. sarawakensis* (77)				++						
94. *T. silvestrii* (26, 65)			++							
95. *T. smithii* (69)			++							
96. *T. terminata* (77)			++							
97. *T. varia* (5)			++							
Trigona, s. str.										
98. *T. amalthea* (Brazil, 20, 29)			++							
98. *T. amalthea* (63, 70)										++
99. *T. chanchamayoensis* (63)							E			
100. *T. c. cilipes* (24, 26, 63)			++				E	ET		
101. *T. corvina* (C. R., 30)										++
102. *T. crassipes* (26)										++
103. *T. dallatoreana* (26, 63)							E			

Table 2 (cont.)

Species and references CR = treated in the section on Costa Rican nests	1. In ground	2. Among roots at foot of tree	3. Tree cavities	4. Slender tubular tree cavities	5. Planiform cavities	6. Artificial cavities	7. In termite nests	8. In ant nests	9. Partly exposed	10. Exposed
104. *T. d. dimidiata* (63)										++
105. *T. f. fulviventris* (C. R., 63)		++								
106 *T. fulviventris guianae* (18, 21, 63)							T	T		
107. *T. fuscipennis* (Colombia, Brazil) (18,21,54,63)			++							
107. *T. fuscipennis* (C.R., 49)							Ec			
108. *T. hyalinata branneri* (49)							++			
109. *T. h. hyalinata* (63)										++
110. *T. hypogea* (63)	++									
111. *T. nigerrima* (C. R.)										++
112. *T. p. pallens* (5, 63, 65)			++				E			
113. *T. recursa* (9, 61)	+	++								
114. *T. silvestriana* (C. R., 63)									+	++
115. *T. spinipes* (18, 21, 29, 63)									++	++
DACTYLURINA										
116. *D. staudingeri* (13)										++

Taibe 2 (cont.)

II – 10

Species and references CR = treated in the section on Costa Rican nests	1. In ground	2. Among roots at foot of tree	3. Tree cavities	4. Slender tubular tree cavities	5. Planiform cavities	6. Artificial cavities	7. In termite nests	8. In ant nests	9. Partly exposed	10. Exposed
LESTRIMELITTA										
Cleptotrigona										
117. *L. cubiceps* (45)			++							
Lestrimelitta, s. str.										
118. *L. ehrhardti* (50)			++							
119. *L. limao* (C. R., 50, 63)			++							
MELIPONULA										
120. *M. bocandei* (44)			++							
MELIPONA										
121. *M. anthidioides* (18, 21)			++							
122. *M. b. beecheii* (C. R., 63)			++							
123. *M. compressipes manaosensis* (26)			++							
124. *M. f. fasciata* (C. R.)			++							
125. *M. fasciata melanopleura* (C. R.)			++							
126. *M. f. favosa* (5)			++			++				

Species and references CR = treated in the section on Costa Rican nests	1. In ground	2. Among roots at foot of tree	3. Tree cavities	4. Slender tubular tree cavities	5. Planiform cavities	6. Artificial cavities	7. In termite nests	8. In ant nests	9. Partly exposed	10. Exposed
127. *M. favosa phenax* (30, 63)						++	+			
128. *M. flavipennis* (C. R.)			++							
129. *M. fuscata melanoventer* (9)			++							
130. *M. interrupta grandis* (9)			++							
131. *M. interrupta triplaridis* (30)						++				
132. *M. marginata amazonica* (26)			++							
133. *M. marginata carrikeri* (C. R.)			++							
134. *M. m. marginata* (18,21,29,56)			++			+				
135. *M. n. nigra* (36)		++								
136. *M. nigra schencki* (18, 21)		++	+							
137. *M. p. pseudocentris* (26)			++							
138. *M. quadrifasciata* (36)	++	++	++							
139. *M. quinquefasciata* (65)			++			++				
140. *M. rufiventris* (18, 21, 29)			++							
141. *M. santhilarii* [1] (3, 20)	++									

(1) This name was used by Ihering and Bertoni for the subterranean, grassland form, otherwise like *M. quinquefasciata*. It is quite likely that different species are incolved although the application of the name *santhilarii* may not be correct.

Table 2 (cont.)

II – 12

Species and references CR = treated in the section on Costa Rican nests	1. In ground	2. Among roots at foot of tree	3. Tree cavities	4. Slender tubular tree cavities	5. Planiform cavities	6. Artificial cavities	7. In termite nests	8. In ant nests	9. Partly exposed	10. Exposed	
142. *M. scutellaris* (29, 55)			++								
143. *M. seminigra abunensis* (9)		++									
144. *M. seminigra merrillae* (26)		++									
UNPLACED											
145. *T. turusiri* (22)			++								

temperature change. Those that nest deep in the soil or in the trunks of large trees are outstanding in this respect. Others can tolerate considerable temperature variation. These are particularly the species that occur in all sorts of cavities in association with human habitations, such as *T. fuscobalteata, iridipennis, jaty*, and *emerina*. A colony of the last in Curitiba, Brazil, withstood outside temperatures ranging from –6°C to 45°C measured on the surface of a nest box of ordinary boards (**Moure, Nogueira–Neto** and **Kerr** 36).

The numbered paragraphs below explain the similarly numbered columns of Table 2.

1. Nests in the ground commonly so modify the cavities used that the original maker of the cavity is difficult to determine. However, abandoned chambers of leafcutter ants (*Atta* and presumably *Acromyrmex*) are sometimes used and are the usual very deep chambers (e.g., 3–5 m below the soil surface) for tropical American subterranean meliponine nests. Species which inhabit *Atta* nests include *Trigona quadripunctata, lineata nuda*, and *subnuda*; some other species which usually nest elsewhere occasionally use *Atta* chambers, e.g., *Melipona quadrifasciata*. Subterranean nests at only moderate depths (less than 1 m) in the soil may occupy abandoned habitations of mammals, as noted for nests of *T. buchwaldi* and *mirandula* (**Wille**, 74), probably abandoned termite fungus gardens in Africa (*T. beccarii*, **Darchen**, 11) or natural crevices among rocks (e.g. *T. buchwaldi*). Species that nest in all sorts of cavities in association with human habitations, such as *T. jaty*, may occasionally nest in the ground.

2. Certain species regularly use subterranean cavities that are among roots at and under the bases of large trees. Whether the cavities were originally made by mammals or by partial rotting is not obvious but such nests are exceedingly well protected from the elements as well as from persons studying bee architecture.

3. Cavities in trees are, of course, extremely variable. Those included under this heading in Table 2 are usually rather large and more or less central in trunks or major branches, commonly near the ground but sometimes at least 15 m above the ground. The cavities are usually rot holes and are ordinarily used by bees only when nearly closed, so that only small apertures permit the entrance of bees. These are the commonest nest sites of the majority of species of stingless bees.

4. By slender cavities in trees we mean the hollows that sometimes rot in aerial roots, small branches, or lianas—cavities usually under 4 cm or thereabouts in diameter but sometimes quite long. Such cavities seem to be the favored nest sities of some species which do not make combs of brood cells.

5. The category called planiform cavities in Table 2 refers to spaces that are so irregular or usually so flat as to prevent construction of combs of cells. Sometimes such cavities are natural rot spaces under the bark of trees; sometimes they are spaces between boards in buildings.

6. Artificial cavities, as used in Table 2, include a miscellany of small man–made enclosures that are not especially slender or flat. This includes cavities in old stone walls, small containers, pieces of sewer pipe, or any of a multitude of similar sites. Of course no species is restricted to such places, and perhaps any species may on occasion utilize a properly placed artificial cavity, but some species utilize such situations so readily that they commonly occur in towns and cities.

7. 8. Associations of Meliponini with termites and ants are well known. For some species they are occasional events, for others, regular or invariable relationships. The bees construct their nests inside those of the ants or termites. Use of abandoned nests of termites or ants is ordinarily not considered justification for recording a species in these columns. Some species listed in paragraph 1 (and column 1 of Table 2) regularly use abandoned *Atta* nests, for example, but we assume that this is merely a response to available cavities in the soil. Species listed in columns 7 and 8 make nests in occupied termite and ant nests. In some cases the bees get into cavities made in aerial termite nests by birds (*Trigona nebulata komiensis* in Gabon, *Trigona fuscipennis* in Costa Rica). In the latter species the termites are sometimes entirely gone (figs. 131–132a). The former and related forms (e.g. *denoiti)* also enter subterranean termite nests, or at least make subterranean nests associated with termites (**Smith**, 67). Such bees' nests probably are in abandoned fungus cavities of the termite nests, not in cavities made by vertebrate animals. Other species of *Trigona* make nests inside of intact nests of termites and ants. Examples are *T. latitarsis* (regularly in aerial *Nasutitermes* nests) and *T. peltata peltata* (often in aerial *Camponotus* nests). Such bees must make their own cavity in the material of the termite or ant nest. We have seen entrances of *T. latitarsis* built on the outsides of *Nasutitermes* nests and assume that from such entrance tubes the bees can extend their occupation into the termite nest and can wall off an area in the interior for their use. Such activity probably precedes the arrival of the queen. The second nest of *T. cilipes cilipes* described by **Kerr,** *et al.* (26) supports this view for it consisted, in addition to an entrance tube, of two small cavities in a termite nest, with a few storage pots each, but without combs. There was no queen. Although lined with batumen, presumably a necessity to exclude the termites, the cavities would presumably be enlarged until space for combs was formed, at which point a young queen would presumably come from the parent nest.

9. All the nest locations listed above are cavities with small openings through which the bees pass. However, some species of *Trigona* are able to close over less fully enclosed spaces, thus making one or more walls of the cavity themselves. For example, *T. braunsi* (=? *gribodoi*), which usually inhabits small irregular or planiform enclosed spaces, sometimes walls over a large crevice in the bark of a contorted tree (**Bassindale**, 1). *Trigona cupira*, while sometimes nesting in enclosed cavities, often builds in partly open situations such as between the bases of palm leaves, in niches in cliffs, banks or walls of buildings, under overhanging parts of buildings, and the like where one to three or more sides of the nest have to be constructed by the bees. If built in the open, nests of this and related species

Table 3. **Costa Rican nests studied. (Parenthetical material concerns nests not studied in detail; dimensions of occupied parts of cavities are given with diameter first, height second. Species are numbered to correspond with other tables.)**

Name	No. of nests	Localities	Sites
12. *T. frontalis*	2	14 km. N of Quepos, Puntarenas Prov.; Pozo Azulon Rio Parrita at San José Prov. border	Forest. Tree cavities 6.5 x 26 and 5.5 x 74.5 cm, 2 m above ground in living trees 20–40 cm in diameter.
18. *T. sp. A*	2	Playón de Aguirre, N of Parrita, Puntarenas Prov.	Disturbed area. Tree cavities, 15 x 66 cm and ± 15 x 50 cm, 1 and 15 m above ground, in dead log and living Cachimbo tree 36 cm in diameter at nest.
21. *T. tica*	2	Playa del Coco, Guanacaste Prov.	Disturbed area. Cavity 2–5 cm in diameter, 26–55 cm long in dead logs used in house construction, 0.2–1.5 m above ground.
22. *T. mirandula*	4	14.5 km. N of Quepos, Puntarenas Prov.	Undisturbed forest. Subspherical soil cavities about 20 cm in diameter, upper surfaces 30–35 cm deep. Old mammal nests.
29. *T. atomaria*	1	17.8 Km N Florencia, San Carlos area, Alajuela Prov.	In forest. Long hollow, 4–5 cm in in diameter, in living tree 7 cm in diameter, 1–2 m above ground.

30. *T. buyssoni*	2	On Pan-American Hwy. 32.3 Km NE Palmar Sur, Puntarenas Prov.; Valle de El General	Disturbed forest. Cavity 0.6 1.2 cm in diameter, 65 cm long, one a cerambycid burrow through horizontal live woody stem 2 m above ground.
34. *T. sp. B*	1	Pozo Azul on Rio Parrita at San José Prov. border	Forest. Tree cavity 8 cm in diameter and 90 cm long 1 m above ground in tree about 30 cm in diameter.
35. *T. latitarsis*	1	San Isidro del General, San José Prov.	Disturbed area. Cavity irregular, 6 x 10 cm, in *Nasutitermes* nest 40 x 50 cm, about 1.7 m above ground.
39. *T. cupira*	6	Localities in San José and Puntarenas Provinces	Disturbed areas. Between bases of palm leaves, in abandoned bird nest, in holes in roadside earth bank. Nests in cavity in soil to almost fully exposed, 0–3 mm above ground, 21–29 cm in diameter.
42. *T. testacea musarum*	1	Beverly near Limón, Limón Prov	Disturbed area. In abandoned bird's nest, exposed except for incorporated plant material, 2 m above ground, 18 x 21 cm diameter.
45. *T. guatemalensis*	1	Rio Navarro near Orosi, Cartago Prov.	Disturbed area. Exposed, 9 x 13 cm, on branch of guava 2 m above ground.
49. *T. ornaticeps*	1	Cerro Nara, east of Quepos, Puntarenas Prov.	Disturbed forest. Nest in cavity 15 x 34 cm in rotting *Cecropia* log.
51. *T. p. peltata*	10	San Isidro del General, San José Prov.; San Antonio de Damas, 14 km. N of Quepos, Puntarenas Prov.	Coffee plantions, etc. In nests of *Camponotus senex* or partially exposed in leaves, 6.5 x 11 cm to 8 x 13 cm, 0.5–15 m above ground.
55. *T. mexicana subobscuripennis*	2	San José and Gromaco on Río Coto Brus, Puntarenas Prov.	City and forest. Tree cavities or large bamboo, 8 x 59 to 20 x 40 cm, 1.5–3 m above ground.

57. *T. pectoralis*	2	Beverly near Limón, Limón Prov.; Orosi, Cartago Prov.	Disturbed areas. Cavities, 1.5–4 m above ground in large trees.
61. *T. mellaria*	1	14 km. N Quepos, Puntarenas Prov.	Forest. Tree cavity, 12 x 29.5 cm, in tree 30 cm in diameter, 4 m above ground.
62. *T. testaceicornis perilampoides*	3	Playa del Coco, Guanacaste Prov.; Gromaco on Rio Coto Brus, Puntarenas Prov.; Common, many places	Disturbed areas. Tree cavities (cavities in logs, masonry walls, etc.). Cavity 14 x 97 cm (but not always elongate), 0.5–4 m above ground.
64. *T. capitata zexmeniae*	1	Playón de Aguirre N of Parrita, Puntarenas Prov.	Disturded area. Tree cavity 20 x 131 cm, 1.4 m above ground in dead trunk of *Pithecolobium saman* 70 cm in diameter.
67. *T. tataira mellicolor*	2	Playón de Aguirre N of Parrita, Puntarenas Prov.	Disturbed area. Tree cavities 33 x 40 and 16 x 54 cm, 2 and 4.6 m above ground in trunks of living trees (one was *Ochroma velutina* 40 cm in diameter).
71. *T. buchwaldi*	3	14.5 km. N of Quepos, Puntarenas Prov.	Undisturbed forest. Subspherical soil cavities 20–23 cm in diameter, 15–30 cm deep. Old mammal nests.
75. *T. dorsalis*	1	14.5 km. N of Quepos, Puntarenas Prov.; Pocares, near Parrita, Puntarenas Prov.	Forest and disturbed area. Tree cavity 12.5 x 47 cm, 0.2 m above ground in trunk of living tree; cavity 30 x 17 cm in soil under roots of tree.
85. *T. j. jaty*	5	Localities in San José, Puntarenas, Cartago, and Limón Provinces	Disturbed areas including cities. Tree cavities, cavity in log, box (spaces in masonry walls).

			Dimensions of representative cavities 8.5 x 20, 5 x 110 (and 15 x 15) cm; height above ground 0–1.5 m.
87. *T. leucogastra chiriquiensis*	1	Mata Limón, Puntarenas Prov.	Disturbed area. Over 1.5 m deep in ground. (Nest proper not reached).
90. *T. nigra paupera*	2	Playa del Coco, Guanacaste Prov.	Disturbed area. Cavity 6 x 156 cm in partially shaded fencepost, cavity extending below ground surface in post; another in largely buried root.
91. *T. perangulata*	1	Playas de Dominical, Puntarenas Prov.	Disturbed area. Tree cavity 25 x 50 cm, 7 m above ground in living *Ficus* tree.
101. *T. corvina*	5	Localities in San José and Puntarenas Provinces	Forest and disturbed areas, even in city. Exposed nests, 34 x 43 to 55 x 85 cm, in trees 2–9 m above ground.
105. *T. f. fulviventris*	1	Localities in San José, Cartago, and Guanacaste Provinces	Disturbed areas. Soil cavity 45 x 22 cm under base of tree. Entrance among roots at ground level (or up to 2 m above ground between buttresses of large tree or in ground at former location of a tree; nest cavity probably sometimes in trunk).

107. *T. fuscipennis*	2	Playón de Aguirre N of Parrita, Puntarenas Prov.; Playa del Coco, Guanacaste Prov.	Disturbed areas. Cavities 20 x 26 and 22 x 29 cm excavated by birds in *Nasutitermes* nests 30 x 36 and 30 x 55 cm, 2–3 m above ground.
111. *T. nigerrima*	2	Playón de Aguirre N of Parrita, Puntarenas Prov.; Pandora, Limón Prov.	Disturbed areas. Exposed nests 27 x 35 and 35 x 46 cm, in trees 10 and 14 m above ground.
114. *T. silvestriana*	2	Beverly near Limon, Limón Prov.; Orosi, Cartago Prov.	Disturbed areas. Irregular exposed nests 52 x 39 and 46 x75 cm resting on large branch or between coconut leaf bases 3–12 m above ground.
119. *L. limao*	1	14 km. N of Quepos, Puntarenas Prov.	Forest (disturbed to suburban areas). Tree cavity 21 x 60 cm 3–5 m above ground in trunk 75 cm in diameter.
122. *M. b. beecheii*	1	Playón de Aguirre N of Parrita, Puntarenas Prov.	Disturbed area. Tree cavity 73 x 10 cm. Cavity in old cut branch 16 cm in diameter.
124. *M. f. fasciata*	2	Puerto Viejo, Sarapiquí, Heredia Prov.; Pandora, Limón Prov.	Disturbed area and forest. Tree cavities 20 x 75 and 20 x 90 cm, 1 m above ground in living trees 45 cm in diameter.
125. *M. fasciata melanopleura*	1	14 km. N of Quepos, Puntarenas Prov.	Forest. Tree cavity 12 x 83 cm, 6 m above ground in living tree 23 cm in diameter.

128. *M. flavipennis*	1	Cerro Nara, east of Quepos, Puntarenas Prov.	Disturbed forest. Tree cavity in recently cut log.
133. *M. marginata carrikeri*	1	Pozo Azul on Rio Parrita at San José Prov. border	Forest. Tree cavity 8 x 60 cm, 2 m above ground in living tree 30 cm in diameter.

usually or always are under dense clumps of epiphytes which provide protection from rains.

10. Some species construct nests fully in the open, supported by the branches of trees. The bees, thus, make their own cavity by means of batumen sheets; the construction inside is much the same as if the nest were built in a pre–existing cavity.

B.— Sites of Costa Rican Nests Studied. Table 3 gives information on the sites of the nests that we have studied in Costa Rica.

NEST STRUCTURES

A.— Terminology and Nest Organization.

1. **Materials:** The materials used in construction of nests of Meliponini are varied, as indicated in the following list:

Cerumen A mixture of wax and propolis. This is the principal construction material. It varies from soft, usually light brown material, probably largely wax, to rigid and even brittle, dark brown or black material.

Propolis—Resins and gums collected in the field and brought to the nest. Probably used for some construction in pure form although presence or absence of a wax admixture has not been determined in most cases. Wet paint, petroleum products, etc., sometimes collected are used in the same way.

Wax—Secretion of the bees. Almost never used in its pure form (Nogueira–Neto in **Michener**, 32).

Mud—Used by relatively few species, probably mixed with propolis or cerumen, for batumen plates and occasionally for entrances.

Feces—Feces of animals and man are used in preference to mud by some species, mostly for outer layers of batumen of exposed nests.

Plant fibers and chewed leaf material: Used by a few species, principally in outer layers of batumen of exposed nests. Some of the pieces of plant material are tender green leaves, in other cases they are bits and fibers removed from dung of animals such as cattle.

Gums and resins collected by stingless bees come from many sources–natural secretions of plants and those that accumulate where plants are cut or diseased, as well as, for some species, products of human activity like freshly applied paint (*T. hockingsi*). However, various species, especially in the subgenus *Trigona*, encourage secretion of gums and resins by biting buds, young leaves, flowers, and bark of various plants, and carrying away the material that exudes. Considerable damage may result, including such things as holes in pine stems (for numerous references, see **Silva** *et al.*, 64). A few species also use chewed leaf material along with propolis or other materials and thus carry away large quantities of young leaves. An example of such damage in Costa Rica is described by **Camacho** (8).

2. **Organization and terminology:** The following is a statement of the basic organization of a meliponine nest in which the terminology used in subsequent sections is explained. Fig. 1 shows the positions of major structures.

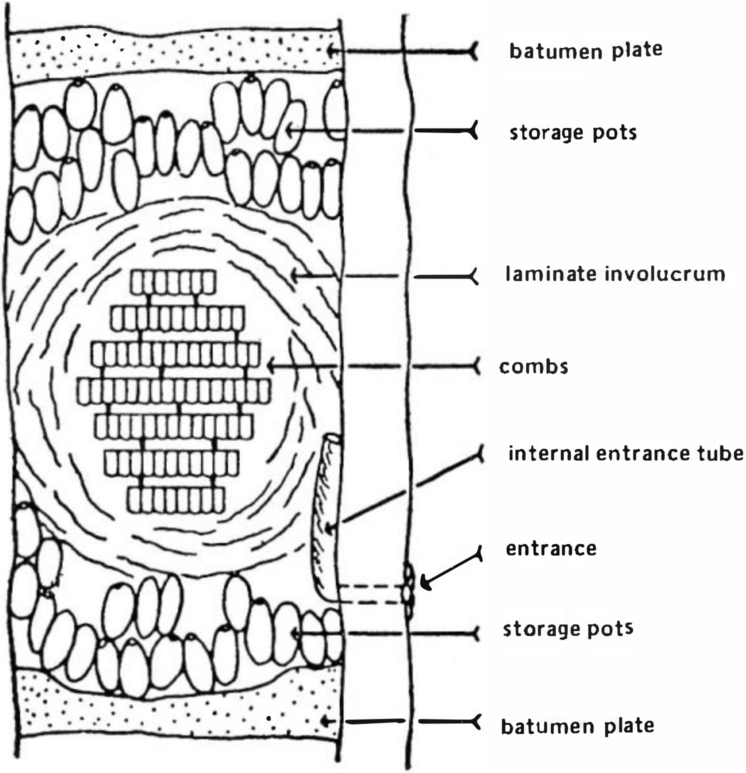

Figure 1. Diagram of meliponine nest with structures labeled. (Modified from *Nogueira–Neto*, 41).

The *batumen* is a protective layer of propolis or hard cerumen (sometimes vegetable matter, mud, or various mixtures) enclosing the nest cavity. The batumen seals the nest cavity except for the entrance and sometimes ventilating perforations. Most commonly it consists of *batumen plates* closing off portions of a natural cavity from the nest cavity, and *lining batumen* which is a thin layer of propolis or cerumen, rarely partly mud, on the walls of the nest cavity. Occasionally a nest without any lining batumen is found. This is the usual condition for some species of *Hypotrigona* and *Trigonisca*; otherwise and possibly even for these two subgenera it is a feature of new nests. Exposed and partly exposed nests are entirely or partly surrounded by *exposed batumen. Laminate batumen* consists of several layers, with spaces between them in which bees can move about. Laminate batumen is usually exposed. (Batumen is a Brazilian word meaning "wall", used by Ihering and subsequent authors, chiefly for the batumen plates.)

The *entrance* is the external opening of the nest for coming and going of the bees. It is often extended outside the nest and its substrate, as an *external entrance tube*. It is also often continued inside the nest cavity, usually along the inner wall of the cavity, as an *internal entrance tube*. Between the external and internal entrance tubes, except in exposed nests, there is in most situations a tube or passageway through the substrate.

The *storage pots* are the containers made of soft cerumen for the storage of honey (honey pots) or pollen (pollen pots).

Pillars and connectives support all nest structures within the batumen. Often they are made of soft cerumen, but close to the batumen, especially at the bottom of the nest, they are usually thickened and brittle. Pillars are more or less vertical. When more or less horizontal, such structures are called connectives. There is no real distinction in kind between pillars and connectives.

The brood chamber is commonly surrounded by an *involucrum*, a sheath of usually, but not always, soft cerumen surrounding and forming the brood chamber. A *laminate involucrum* consists of several layers with spaces between them in which bees can move about. In species having the involucrum and batumen both laminate, it often happens that the sheets are similar or intergrade in aspect. The only distinction is that the storage pots are inside of the batumen and outside of the involucrum. Sometimes they are intermingled with some of the sheets, so that a decision as to the name to be used for a particular sheet is arbitrary. The expression *enveloping sheets* may be used for the batumen and involucrum taken together and is particularly appropriate when they are alike in appearance and merge one into the other, especially in parts of the nest where there are no storage pots. Earlier literature uses the word involucrum broadly, to include the sheets here called exposed and laminate batumen. **Nogueira–Neto** (39) and **Nogueira–Neto** and **Sakagami** (42) used outer involucrum or exoinvolucrum for what is here called exposed or laminate batumen and inner involucrum or endoinvolucrum for what is here called simply the involucrum. The terminology here utilized was introduced by **Michener** (32), because the material surrounding the nest seemed comparable whether consisting of a single layer applied to the walls of a cavity (lining batumen) or closing off parts of a cavity (batumen plates) or of single or multiple layers built around the space to be used for the nest. Indeed in partially exposed nests such as those of *T. cupira* the continuity of exposed and laminate batumen with lining batumen is readily demonstrable.

The *brood chamber* is the cavity containing the brood cells. The *brood cells* are made of soft cerumen. In each a single young is reared. Each cell is fully provisioned before egg laying with a mixture of pollen, honey, and secretions of the hypopharyngeal glands. Then an egg is laid by the queen and the cell is closed. The fascinating details of the provisioning and laying have been described by Sakagami and his colleagues (see **Sakagami** and **Zucchi**, 51). The cells are in contact with one another or connected by small pillars or connectives of soft cerumen; such pillars connect groups or layers of cells with one another and with surrounding structures.

The *cocoons* are silk structures spun by the mature larvae around the inner walls of the cells. The worker bees remove and reuse much of the cerumen of which the cells are constructed, leaving the cocoons largely exposed during the prepupal and pupal periods.

A *cluster* (of cells or cocoons) is a group of brood cells or cocoons irregularly arranged, not in combs.

A *comb* (of cells or cocoons) is a layer of brood cells or cocoons crowded together.

The *advancing edge* of a comb is the margin to which new cells are being added.

The *advancing front* is the surface in the cell cluster or group of combs which advances because of the addition of new cells.

B.– Tabular Sumary of Meliponine Nest Structure

1. **Content and methods**: Tables 4 and 5 summarize the data on meliponine nests from literature and from our own notes. It is obvious that many aspects of nest structure cannot be communicated by a tabular presentation. Excellent illustrations such as those of **Camargo** (9) are the best method of showing structural detail. Yet no two nests, even when made by bees of the same species and in the same locality, are alike. They vary according to the immediate environment, colony size, age, and other matters, quite aside from such genetic differences as may cause differences in nest construction. Moreover, it is impractical to provide excellent illustrations of each nest, and at the moment it is impossible to do so for each species because of lack of data. The tabular summary does not exclude individual differences between nests. Too few nests of most species have been studied to permit firm generalization. But at least for the better known species the tables hopefully emphasize some of the specific and group similarities and differences.

The columns in the tables are by no means a complete list of the things that should be recorded in describing a meliponine nest. Other items are discussed below. But at least the column headings in the tables list some of the things that should not be omitted from future accounts of nests. One of the disappointments of our sources of information, both the published literature and our own notes, is the frequency with which important details have not been observed or recorded. Even for some of the behaviorally best studied species, accounts of nest structure are extremely fragmentary or old, inconsistent, with identifications and data unverfied.

Table 4. Characteristics of the nests. Symbols are explained in the text, the column numbers referring to numbered explanatory paragraphs.

	Entrance											Batumen			
Species and references CR = treated in the section on Costa Rican nests	1. Length	2. Shape	3. Rigidity	4. Ornaments	5. Perforation	6. Lip	7. Night closure	8. Radiating ridges	9. Size	10. 2 or more entrances	11. Internal tube	12. No. of layers	13. Lining	14. Plates	15. Plant or fecal material
TRIGONA															
Meliplebeia															
1. *T. beccarii* (43, 68)	+	C	H	A	–	Th	–*	–	++	–	–	1	+	NC	NC
2. *T. d. denoiti,* etc. (67, 68)	–,+	C*,NC		A,NC	–,NC			–		–		1?	+	NC	NC
3. *T. lendliana* (46)	+,++	C	S	A	–*	Th	+	–	+	–	++	1	++	NC	NC
5. *T. nebulata komiensis* (6, 11)	+	F	H*	A	–*	T	–*	–	+	–	+	1	++	NC	NC
6. *T. tanganyikae medionigra* (46)	+	C		A	–*	Th*		–	+	–	++	1	++	NC	NC
Plebeia															
7. *T. australis* (32)	+,++	C	S	A	+	Th	+	–	+	–	++	1	+*	C	NC
8. *T. cincta* (32)	++	C	S	A	+	Th	+	–	+,++	–		1	+*	C	NC
9. *T. domiciliorum* (47)	++	C	S*	A*		Th*	+	–	–	–					NC
10. *T. droryana* (18, 21, 29, 65)	–	NC	NC	NC	NC	NC	–	–	–	+	+				NC
11. *T. emerina* (18, 21, 36, 56)	+	C	S	A		Th		–	+	+		1*	+		NC
12. *T. frontalis* (C.R.)	–	NC	NC	NC	NC	NC		–	–	–	–	1	+	–,C	NC
13. *T. minima* (4, 63)	–	NC	NC	NC	NC	NC		–*	+	–					NC

	Entrance											Batumen			
	1. Length	2. Shape	3. Rigidity	4. Ornaments	5. Perforation	6. Lip	7. Night closure	8. Radiating ridges	9. Size	10. 2 or more entrances	11. Internal tube	12. No. of layers	13. Lining	14. Plates	15. Plant or fecal material
15. *T. mosquito* [1] (18, 21, 29)	+,++											1*	+*	C	NC
17. *T. q. quadripunctata* (18, 21, 29, 63)	–,+	C,NC	H,NC	A,NC	–,NC	Th,NC	–*	–	++	–		1–sev.	++,NC		NC
18. *T. sp. A* (C.R.)	–	NC	NC	NC	NC	NC		–	–	+	–	1	+	NC	NC
19. *T. remota* (36)	–	NC	NC	NC	NC	NC		–	+	–					NC
20. *T. schrottkyi* (18, 21, 29, 36, 63)	–,+	NC		A*			+	–	+	–		1*	+*	C	NC
21. *T. tica* (C.R.)	–	NC	NC	NC	NC	NC	+	–	–	–	++	1	±	C	NC
Nogueirapis															
22. *T. mirandula* (C.R.)	+	C	S	A	++	Th	+	–	+	–	+	1	++	NC	NC
Axestotrigona															
23. *T. eburnensis* (12)											–	1	+	NC	NC
24. *T. sawadogoi* (12)	–	NC	NC	NC	NC	NC		–	+	–	–	1	+	NC	NC
25. *T. togoensis* (15, 44, 67, 68)	–,++	C,NC	H,NC	A,NC	–,NC	Th,NC	+	–	+	–					NC

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[1] Ihering's (18, 21) nests may have belonged to more than one species.

Table 4 (cont.)

		Entrance											Batumen			
		1. Length	2. Shape	3. Rigidity	4. Ornaments	5. Perforation	6. Lip	7. Night closure	8. Radiating ridges	9. Size	10. 2 or more entrances	11. Internal tube	12. No. of layers	13. Lining	14. Plates	15. Plant or fecal material
	Hypotrigona															
26.	*T. araujoi* (31, 44)	++	C		A	–	Th		–	++	–		1		C	NC
27.	*T. braunsi* (1, 31, 44)	++	C		A	–	Th		–	+	–	+	1		C	NC
28.	*T. gribodoi* (43)	++	C	S	A	–	Th		–	+	+	+,–	1	–	–,C	NC
	Trigonisca															
29.	*T. atomaria* (C.R.)	–	NC	NC	NC	NC	NC	–*	–	+	–	–	NC	–		NC
30.	*T. buyssoni* (C.R.)	–	NC	NC	NC	NC	NC	–*	–	+	–	+	NC,1	–,+	–,C	NC
31.	*T. duckei* (59)															NC
33.	*T. muelleri* (19, 63)												1*		–	NC
34.	*T. sp. B* (C.R.)	–	NC	NC	NC	NC	NC	–*	–	+	–	–	NC	–?	–	NC
	Scaura															
35.	*T. latitarsis* (C.R., 9, 30, 63)	++	C	S	A	+	Th	+	–	+	–	–	1	++	NC	NC
36.	*T. longula* (63)	++	C		A		Th*		–		–					NC
37.	*T. tenuis* (26)	++	T	S	A	–	Th		–	+	–					NC
38.	*T. timida* (63, 65)	++	C		A*	+			–	+	–					NC

	Entrance											Batumen			
	1. Length	2. Shape	3. Rigidity	4. Ornaments	5. Perforation	6. Lip	7. Night closure	8. Radiating ridges	9. Size	10. 2 or more entrances	11. Internal tube	12. No. of layers	13. Lining	14. Plates	15. Plant or fecal material
Partamona															
39. *T. cupira* (C.R., 18, 21, 30)	–,+	F	H	A,L	–,NC	C,T	–	–	++	+	–	1–9	++,NC	NC	±
41. *T. testacea helleri* (18, 21, 29)	+	F	H	A	–*	T	–*	–	++	+		sev.	NC	NC	+
42. *T. testacea musarum* (C.R.)	+	F	H	A	–	T	–*	–	++	+	–	3–6	NC	NC	–
43. *T. testacea orizabensis* (48)	–?	F	H	A	–	T	–*	–	++	+				NC	+
44. *T. t. testacea* (9, 26)	+,++	F C,F	H	A	–	T,Th	–*	–	++	–	–	1–2	++,NC	NC	NC
Partatrigona															
45. *T. guatemalensis* (C.R.)	+	F	S	A	+	Th		–	+	–	–	1	NC	NC	–
46. *T. impunctata* (59, 63)												1	++	NC	NC
47. *T. isopterophila* (63)	–	NC	NC	NC	NC	NC		–	–	–					NC
48. *T. lineata nuda* (62)												1?	+	NC	NC
49. *T. ornaticeps* (C.R.)	+	I	H	A	–	T	–*	–	++	–	–	1	+	C	NC
50. *T. peltata pacifica* (63)															NC
51. *T. p. peltata* (C.R.)	++	C	S	A	+	Th	+	–	+	–	–	1	NC	NC	–,NC
52. *T. subnuda* (18, 21, 36, 63)	+	C*		A*	+		+	–	++	–					NC

Table 4 (cont.)

	Entrance											Batumen			
	1. Length	2. Shape	3. Rigidity	4. Ornaments	5. Perforation	6. Lip	7. Night closure	8. Radiating ridges	9. Size	10. 2 or more entrances	11. Internal tube	12. No. of layers	13. Lining	14. Plates	15. Plant or fecal material
Scaptotrigona															
53. *T. bipunctata* or *postica* (20)	++	C	H	A		Th		–	++	+				C	NC
54. *T. iheringi* (18, 21)	++	C	F	A	++	Th		–	++	+					
55. *T. mexicana subobscuripennis* (C.R.)	+	C,F,I	F	A	–,+	Th		–	++	–	+	1	+	C	NC
56. *T. pachysoma* (30)	++	C	F*	A		Th*	–	–	++	–					NC
57. *T. pectoralis* (C.R., 63)	++	C,I	F	A	++	Th		–	++	+					NC
58. *T. postica* (26, 63)										+					NC
59. *T. tubiba* (18, 21, 36)	–?									++					NC
60. *T. xanthotricha* (9)	++	C		A	+	Th		–	++	–					NC
Nannotrigona															
61. *T. mellaria* (C.R.)	++	C	H?	A	++	Th		–	++	–	–	1	+	C	NC
62. *T. testaceicornis perilampoides* (C.R., 30)	+,++	C	S	A	++	Th	+	–	++	–	–	1	+	C	NC
Cephalotrigona															
63. *T. c. capitata* (20, 54, 63)	–	NC	NC	NC	NC	NC	–*	–	–	–				C,M	NC
64. *T. capitata zexmeniae* (C.R., 63)	–	NC	NC	NC	NC	NC	–*	–	–	–	+,++	1	±	C, $\frac{C}{M}$	NC
65. *T. femorata* (26)	++	C		A	–*			–	++	–	+?	1*	+*	C	NC

Table 4 (cont.)

	Entrance											Batumen			
	1. Length	2. Shape	3. Rigidity	4. Ornaments	5. Perforation	6. Lip	7. Night closure	8. Radiating ridges	9. Size	10. 2 or more entrances	11. Internal tube	12. No. of layers	13. Lining	14. Plates	15. Plant or fecal material
Oxytrigona															
66. *T. obscura* (9)	–	NC	NC	NC	NC	NC	–*	–	–	–		1*		M?	NC
67. *T. tataira mellicolor* (C.R., 63)	–	NC	NC	NC	NC	NC	–*	–	–	+	–	1–2	±,NC	C	NC
68. *T. t. tataira* (3, 18, 21, 63)	–	NC	NC	NC	NC	NC	–*	–	–	–					NC
Tetragona															
69. *T. a. apicalis* (63, 77)	++	C	H	A	–			–		+					NC
70. *T. atripes collina* (69, 77)	++	C	H	A	–			–		–		+	++	C	NC
71. *T. buchwaldi* (C.R.)	+	C	S	A	++	Th	+	–	+	–	+	1	++	NC	NC
72. *T. carbonaria* (32)	–	NC	NC	NC	NC	NC	–	–	+,++	–	++	1–sev.	+,NC	C	NC
73. *T. clavipes* (5, 52)	–	NC	NC	NC	NC	NC		–	+	–	–	1	++	C	NC
74. *T. clypearis* (32)	+,++	C	F	A,S	–	T		–	+,++	–	–	1	+	C [1]	NC
75. *T. dorsalis* (Central Amer.) (C.R., 10, 30, 47)	++	C	H	S	++	Th T		–	+	+	–	1–4	++,NC	C,NC	NC
75. *T. dorsalis* (Amazon) (26)	–	NC	NC	NC	NC	NC		–	+	–	–	1	++	C	NC
75. *T. dorsalis* (S. Brazil) (18, 21)	+	F		A	–	Th	–*	–	+	–		1*	+*	C	NC
76. *T. flavicornis* (26)	–	NC	NC	NC	NC	NC		+	–	–	–	1		C	NC

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[1] Small walls of batumen enclosing space between boards, etc.

Table 4 (cont.)

	Entrance											Batumen			
	1. Length	2. Shape	3. Rigidity	4. Ornaments	5. Perforation	6. Lip	7. Night closure	8. Radiating ridges	9. Size	10. 2 or more entrances	11. Internal tube	12. No. of layers	13. Lining	14. Plates	15. Plant or fecal material
77 *T. freiremaiai* (35)	–*	NC*	NC*	NC*	NC*	NC*		–*	+	–					NC
80. *T. genalis* (32)	+*							–							NC
81. *T. ghilianii* (26)	++	C		A	–	T		–	++	–	–	1?	–?	C	NC
82. *T. hockingsi* (32)	+	C						–	++	–	+	1	+	C	NC
83. *T. iridipennis* (14, 16, 28, 32, 57, 58, 60)	–, +, ++	NC C,F,	F,NC	A,NC	–,NC	T,NC	+	–	++	–	–	1	+	C,NC	NC
84. *T. itama* (77)	++	C	F,S	A	–*	T?		–		–					NC
85. *T. j. jaty* (C.R., 18, 21, 29, 30)	+,++	C	S	A	+	Th	–,+ [1]	–	+	+	–	1	±	C	NC
86. *T. javanica* (16, 60)	++	F	S	A		Th		–	++	–					NC
88. *T. lurida* (9, 26, 71)	–,+	C,NC	H,NC	S,NC	–,NC	Th,T,NC	–*	–	++	–					NC
89. *T. mombuca* (18, 21, 42, 65)	–,+	C,NC		A,NC				–		–		1–few	+,NC	NC	NC
90. *T. nigra paupera* (C.R., 30)	–	NC	NC	NC	NC	NC	–*	–	+	–	–	1	+	C	NC
91. *T. perangulata* (C.R.)	–	F	H	E	NC	T	–*	–	+	–	–	1	+	C	NC

[1] Marianno says the entrance is closed on cold nights and wet days but not on ordinary nights.

		Entrance											Batumen			
		1. Length	2. Shape	3. Rigidity	4. Ornaments	5. Perforation	6. Lip	7. Night closure	8. Radiating ridges	9. Size	10. 2 or more entrances	11. Internal tube	12. No. of layers	13. Lining	14. Plates	15. Plant or fecal material
94.	*T. silvestrii* (20, 35, 63, 65)									–			1	+	C	NC
95.	*T. smithii* (69)												1*	+*		NC
96.	*T. terminata* (77)	+	F	S	A	–	Th		–	++	–					NC
97.	*T. varia* (5, 36, 63)		F													NC
	Trigona, s. str.															
98.	*T. amalthea* (Brazil) (20, 63)	–	NC	NC	NC	NC	NC	–*	–	++*	–		sev.	+*,NC	C*	+,NC
98.	*T. amalthea* (63, 70)	+,++	C,F		A*	–*	T*	–*	–	++	–		7	NC	NC	–,+
99.	*T. chanchamayoensis* (63)	+	C*		A*	–*			–	++	–		1	++	NC	NC
100.	*T. c. cilipes* (26, 63)	++	C	F	S	–	Th		–	++	–	–	1	++	NC	NC
101.	*T. corvina* (C.R., 30, 63)	–	NC	H	NC	NC	NC	–	–	++	–	–	5–10	NC	NC	–
102.	*T. crassipes* (26)	–	NC	NC	NC	NC	NC	–*	–	++	–*		sev.*	NC*	NC	
104.	*T. d. dimidiata* (63)												11?	NC	NC	+
105.	*T. f. fulviventris* (C.R., 63)	–,+,++	F,NC	F,H	A,NC	–,NC	T,NC	–	–	++	–	–	irrg.	NC	NC	NC
106.	*T. fulviventris guianae* (18, 21, 63)	+	F	F,H	A	–	T	–*	–	++	–		irrg.*	NC	NC	NC
107.	*T. fuscipennis* (Colombia) (54, 63)	–	NC	NC	NC	NC	NC	–*	–	++	–	–	1	+*	M	NC
107.	*T. fuscipennis* (C.R., 49)	–,+	F,NC	H	E	–,NC	T,NC	–*	–	++	–	–	1–4	NC	NC	NC

	Entrance											Batumen			
	1. Length	2. Shape	3. Rigidity	4. Ornaments	5. Perforation	6. Lip	7. Night closure	8. Radiating ridges	9. Size	10. 2 or more entrances	11. Internal tube	12. No. of layers	13. Lining	14. Plates	15. Plant or fecal material
110. *T. hypogea* (63)	–	NC	NC	NC	NC	NC		–*	++*	–*					NC
111. *T. nigerrima* (C.R.)	++	C	H	A	–	Th	–	–	++	–	+,++	6–10	NC	NC	+
112. *T. p. pallens* (63, 65)	+	C	H	A	–			–	++	–					NC
113. *T. recursa* (9, 61)	++	F		A	–	Th	–*	–	++	–	–	3	NC	NC	NC
114. *T. silvestriana* (C.R., 37, 63)	+,++	C,F	H	A	–	T	–*	–	++	+	–	3–7	NC	NC	–
115. *T. spinipes* (18, 21, 29, 63)	–	NC	NC	NC	NC	NC	–*	–	++	+	–	sev.	NC	NC	+
DACTYLURINA															
116. *D. staudingeri* (13, 67, 68)	–	NC	NC	NC	NC	NC		–	++	+	–	irrg.	NC	NC	–*
LESTRIMELITTA															
Cleptotrigona															
117. *L. cubiceps* (45)	++	C		A	–	T	+	–	+	–	+	1*	+*		NC
Lestrimelitta, s. str.															
118. *L. ehrhardti* (50)	++	C	F	A	–	Th	–*	–	++	–	–	*Melipona* host			
119. *L. limao* (C.R., 3, 18, 21, 50)	++	C,F	H	L,S	–	T	–*	–	++	–	–	1	++	C	NC
MELIPONULA															
120. *M. bocandei* (44)	–	NC	NC	NC	NC	NC	+	–	++	–		1*	+	C*	NC

	Entrance											Batumen			
	1. Length	2. Shape	3. Rigidity	4. Ornaments	5. Perforation	6. Lip	7. Night closure	8. Radiating ridges	9. Size	10 2 or more entrances	11. Internal tube	12. No. of layers	13. Lining	14. Plates	15. Plant or fecal material
MELIPONA															
121. *M. anthidioides* (18, 21, 29)	–	NC	NC	NC	NC	NC	–*	–*	–	–		1	++	M	NC
122. *M. b. beecheii* (C.R., 2, 7, 63)	–	NC	NC	NC	NC	NC	–	–	–	–	–	1	+	M	NC
123. *M. compressipes manaosensis* (26)	–	NC	NC	NC	NC	NC	–*	++	–	–	–	1	+*	M*	NC
124. *M. f. fasciata* (C.R.)	–	NC	NC	NC	NC	NC	–*	–	–	–	–	1	+	M	NC
125. *M. fasciata melanopleura* (C.R.)	–	NC	NC	NC	NC	NC	–*	–	–	+	–	1	+	M*	NC
126. *M. f. favosa* (5)															NC
127. *M. favosa phenax* (30)	–	NC	NC	NC	NC	NC	–*	–	–	–					NC
128. *M. flavipennis* (C.R.)	–	NC	NC	NC	NC	NC	–	–	–	–	–	1	+	M*	NC
129. *M. fuscata melanoventer* (9)	–	NC	NC	NC	NC	NC	–*	++	–	–					NC
130. *M. interrupta grandis* (9)	–	NC	NC	NC	NC	NC	–*	+	–	+	–	1	+	M*	NC
131. *M. interrupta triplaridis* (30)	–	NC	NC	NC	NC	NC	–*	–	–	–					NC
132. *M. marginata amazonica* (9, 26)	–	NC	NC	NC	NC	NC	–*	++	–	–	–	1	–	M	NC
133. *M. marginata carrikeri* (C.R., 26)	–	NC	NC	NC	NC	NC	–*	–	–	–	–	1	+	M	B
134. *M. m. marginata* (3, 18, 21, 36, 56)	–	NC	NC	NC	NC	NC	–*	–, ++	–	–	–	1	+	M	NC
135. *M. n. nigra* (63)	–*	NC*	NC*	NC*	NC*	NC*	–*								NC

Table 4 (cont.)

	Entrance											Batumen			
	1. Length	2. Shape	3. Rigidity	4. Ornaments	5. Perforation	6. Lip	7. Night closure	8. Radiating ridges	9. Size	10. 2 or more entrances	11. Internal tube	12. No. of layers	13. Lining	14. Plates	15. Plant or fecal material
136. *M. nigra schencki* (3, 18, 21)	–	NC	NC	NC	NC	NC	–*	+, –	–	–		1*		M*	NC
137. *M. p. pseudocentris* (26)	–	NC	NC	NC	NC	NC	–*	++	–	–	–	1	+	M	NC
138. *M. quadrifasciata* (36)	–	NC	NC	NC	NC	NC	–*	++	–	–					NC
139. *M. quinquefasciata* (65)	–	NC	NC	NC	NC	NC	–*	+	–	–					
140. *M. rufiventris* (18, 21)	–	NC	NC	NC	NC	NC	–*	+*	+	–		1	+	M	NC
141. *M. santhilarii* (3, 20)	+	C	H	A	–		–*	–	+	–	–	1		NC	NC
142. *M. scutellaris* (29, 55)	–,+[1]	NC	H,NC	A,NC	–,NC	Th,NC	–*	+	+	–					
143. *M. seminigra abunensis* (9)	+	F	H	A	–	C	–*	–	–	–	–*	1*	+*	M*	NC
144. *M. seminigra merrillae* (26)	+	F	H	A	–	C	–*	–	++	–	–*	1*	+*	M*	NC
UNPLACED															
145. *T. turusiri* (22)	–	NC	NC	NC	NC	NC		–		–	+	+*	+*		NC

[1] Marianno reports a free entrance tube in nests in the field, although as in most *Melipona* it is absent in domestication.

Table 4a. Continuation of Table 4. – Characteristics of the nests.

Species and references CR = treated in the section on Costa Rican nests	Involucrum				Pots					Brood cells			
	16. Presence	17. No. of layers	18. Rigidity	19. Merging with batumen	20. Honey	21. Pollen	22. Pollen & honey in separate clusters	23. Location	24. Shape, brood chamber	25. Shape and synchrony	26. Arrangement	27. No. of combs	28. Pillars
TRIGONA													
Meliplebeia													
1. *T. beccarii* (43, 68)	++	sev.		–	E,S	E,S		A		L	Co	10	S
2. *T. d. denoiti*, etc. (67, 68)	++	sev.		–?	E	E	–			L*	Co*? ,SC	10–14	S
3. *T. lendliana* (46)	++	6–13	H,S	–	E,S	E,S	–	SS	S	L	Co	7	S
5. *T. nebulata komiensis* (6, 11)	+	2–?		–	S	S		S	E	L	SC	4–10	S
6. *T. tanganyikae medionigra* (46)	++	4–10	H*,S*	–	E	E	+	SS	E	L	Co	8–12	S
Plebeia													
7. *T. australis* (32)	+	1	S	–	S	S	+	A,U	L	S	C	NC	NC
8. *T. cincta* (32)	+	1	S	–	S	S	+*	A,U	E	S	CL	NC	NC
9. *T. domiciliorum* (47)											C[1]*		
10. *T. droryana* (18, 21, 29, 65)	+									L*	Co	6	
11. *T. emerina* (18, 21, 36, 56)	+				E	E		U	S	L	Co	6	
12. *T. frontalis* (C.R.)	+,++	1	S	–	E	E	+	A,U	E,S	L,s	Co	5–14	S°
13. *T. minima* (4, 63)											C		
14. *T. molesta* (18, 21, 29)	+	sev.		–	E	E				L	Co	9–20	

[1] Based on Rau's statement that he withdrew cocoons (evidently not grouped in combs) from a nest.

	Involucrum				Pots					Brood cells			
	16. Presence	17. No. of layers	18. Rigidity	19. Merging with batumen	20. Honey	21. Pollen	22. Pollen & honey in separate clusters	23. Location	24. Shape, brood chamber	25. Shape and synchrony	26. Arrangement	27. No. of combs	28. Pillars
15. *T. mosquito* (18, 21, 29)	+	sev.		–*	E	E				L	Co	8–13	
17. *T. q. quadripunctata* (18, 21, 29, 63)					E	E		SS	S	L*	SC	7–8	S
18. *T. sp. A* (C.R.)	–,++	0–2	S,NC	–,NC	E,S	E,S	+	SS^{+}	E	L,s	Co	10–12	S
19. *T. remota* (36)	–	NC	NC	NC						L*	Co*		
20. *T. schrottkyi* (18, 21, 29, 36, 63)	–	NC	NC	NC	S	S		NC	NC	E	IC		
21. *T. tica* (C.R.)	–	NC	NC	NC	E	E	+	NC	NC	E	C	NC	NC
Nogueirapis													
22. *T. mirandula* (C.R.)	+	3–10	H,S	–	E	E	+	U	F	L	Co	5–8	S^{o}
Axestotrigona													
23. *T. eburnensis* (12)	–	NC	NC	NC	S	S		S,U	S	L	Co	10	S
24. *T. sawadogoi* (12)	–	NC	NC	NC	S	S		S	E,S	L	SC	4–5	S
25. *T. togoensis* (15, 44, 67, 68)	+	? –15			E	E	–,+		E	L	Co	1–15	

Table 4a (cont.)

	Involucrum				Pots					Brood cells			
	16. Presence	17. No. of layers	18. Rigidity	19. Merging with batumen	20. Honey	21. Pollen	22. Pollen & honey in separate clusters	23. Location	24. Shape, brood chamber	25. Shape and synchrony	26. Arrangement	27. No. of combs	28. Pillars
Hypotrigona													
26. *T. araujoi* (31, 44)	–	NC	NC	NC	E	E		NC	NC	E	CL	NC	NC
27. *T. braunsi* (1, 31, 44)	–	NC	NC	NC	S	S		NC	NC	E	C	NC	NC
28. *T. gribodoi* (43)	–	NC	NC	NC	S	S	+	NC	NC	E	C	NC	NC
Trigonisca													
29. *T. atomaria* (C. R.)	–	NC	NC	NC	L*	L*		NC	NC	E*	C	NC	NC
30. *T. buyssoni* (C. R.)	–	NC	NC	NC	L*	L		NC	NC	E,a	C	NC	NC
31. *T. duckei* (59)	–*	NC*	NC*	NC*				NC	NC	E	C	NC	NC
33. *T. muelleri* (19, 63)	–*	NC*	NC*	NC*	S	S		NC	NC	E	C	NC	NC
34. *T. sp. B* (C.R.)	–	NC	NC	NC	L	L		NC	NC	E	C	NC	NC
Scaura													
35. *T. latitarsis* (C.R., 9, 30, 63)	–,+ [1]	NC	NC	NC	S	S	+	A,U	E,F	L,a	Co	4–8	S
36. *T. longula* (63)	+									L*	Co		
37. *T. tenuis* (26)													
38. *T. timida* (63, 65)					E	E		NC	NC	S	C	NC	NC

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[1] No details are available as to the involucrum reported by Ducke (see Schwarz, 63)

	Involucrum				Pots					Brood cells			
	16 Presence	17. No. of layers	18. Rigidity	19. Merging with batumen	20. Honey	21. Pollen	22. Pollen & honey in separate clusters	23. Location	24. Shape, brood chamber	25. Shape and synchrony	26. Arrangement	27 No. of combs	28. Pillars
Partamona													
39. *T. cupira* (C.R., 18, 21, 30)	+	1–7	H,S	++	E	E	+	A,R,S,U	E,L,S	L,a	Co	5–16	LL
41. *T. testacea helleri* (18, 21, 29)	+	2		++	E,S	E,S		U	S	L	C	10	
42. *T. testacea musarum* (C.R.)	+	2–3	S	++	E,S	E,S		U	E	L,a	Co	14	LL
43. *T. testacea orizabensis* (48)										L*	Co	12	
44. *T. t. testacea* (9, 26)	–,+	0–6	H,S,NC	++,NC	E	E		S,U	E,S	L	Co	11	LL
Partatrigona													
45. *T. guatemalensis* (C.R.)	++	2–5	S	+	E	E		$\frac{S}{U}$	S	L,s	Co	11	S^+
46. *T. impunctata* (59, 63)	–	NC	NC	NC	S	S		U	F	L	Co	3	S
47. *T. isopterophila* (63)													
48. *T. lineata nuda* (62)	++	many		+				U	E	L	Co	7	S
49. *T. ornaticeps* (C.R.)	++	7–9	H,S	–	E	E	+	R	E	L,s?	Co	20	S^+
50. *T. peltata pacifica* (63)										L	Co*	10	
51. *T. p. peltata* (C.R.)	++	1–5	S	+	S	S		U	S	L,a	Co	9–10	S^+
52. *T. subnuda* (18, 21, 36, 63)	++	sev.			E	E		S		L*	Co		

	Involucrum				Pots					Brood cells			
	16. Presence	17. No. of layers	18. Rigidity	19. Merging with batumen	20. Honey	21. Pollen	22. Pollen & honey in separate clusters	23. Location	24. Shape, brood chamber	25. Shape and synchrony	26. Arrangement	27. No. of combs	28. Pillars
Scaptotrigona													
53. *T. bipunctata* or *postica* (20)					E,S	E,S				L	Co,SC	17	
55. *T. mexicana subobscuripennis* (C.R.)	++	3–6	S	+	E,S	E,S	+	A,S,U	E	L	Co	7–19	S
58. *T. postica* (26, 63)											IS	27–40	
59. *T. tubiba* (18, 21, 36)					E	E		A,U		L	Co	20	
60. *T. xanthotricha* (9)	++			—				A,U					
Nannotrigona													
61. *T. mellaria* (C.R.)	++	4	S	–	S	S	+	SS$^+$	F,S	L,a	Co	13	S°
62 *T. testaceicornis perilampoides* (C.R., 30)	++	1	S	–	S	S		A,U	F	L	Co	11	S
Cephalotrigona													
63. *T. c. capitata* (20, 54, 63)	++	many		–*	E	E		A		L	Co,IC		
64. *T. capitata zexmeniae* (C.R., 63)	+	1–3	S	–	E	E	+	R	E	L,a	Co	18–19	S°
65. *T. femorata* (26)	+	1–2		–*	E	E			E	L	Co	17	

	Involucrum				Pots					Brood cells			
	16. Presence	17. No. of layers	18. Rigidity	19. Merging with batumen	20. Honey	21. Pollen	22. Pollen & honey in separate clusters	23. Location	24. Shape, brood chamber	25. Shape and synchrony	26. Arrangement	27. No. of combs	28. Pillars
Oxytrigona													
66. *T. obscura* (9)	++							A,U					
67. *T. tataira mellicolor* (C.R., 63)	++,+	1	H,S	–	E	E	–	R	E	L,a	SC $\frac{SC}{Co}$	20–29	S°
Tetragona													
69. *T. a. apicalis* (63, 77)											C	NC	NC
70. *T. atripes collina* (69, 77)	++	sev.		+	E,L	E,L				E	C	NC	NC
71. *T. buchwaldi* (C.R.)	++	3–6	H,S	–	L	L	++	S,U	E	L,a	Co	11–14	S^+
72. *T. carbonaria* (32)	++	sev.	S	++	S	S	+	A,R		L	SC	17	S
73. *T. clavipes* (5, 52)	++	5–7	H,S	–	E	E		A,U	E	L	Co	20	S
74. *T. clypearis* (32)	–	NC	NC	NC	E	E		NC	NC	E	C	NC	NC
75. *T. dorsalis* (Central Amer.) (C.R., 10, 30, 47)	++	1–4	H,S	–,+	E	E	+	A,U	E,S	L,s?	SC	17	S
75. *T. dorsalis* (Amazon) (26)	+	1		–	E	E		R	S	L	Co,IS	10	S
75. *T. dorsalis* (S. Brazil) (18, 21)	+				E	E	+	A,U	E,L	L	Co? ,IS	4–27	
76. *T. flavicornis* (26)	–	NC	NC	NC	E,L	L	+	NC	NC	L	C	NC	NC

Table 4a (cont.)

	Involucrum				Pots					Brood cells			
	16. Presence	17. No. of layers	18. Rigidity	19. Merging with batumen	20. Honey	21. Pollen	22. Pollen & honey in separate clusters	23. Location	24. Shape, brood chamber	25. Shape and synchrony	26. Arrangement	27. No. of combs	28. Pillars
77. *T. freiremaiai* (35)	–	NC	NC	NC	E,L	L		NC	NC	L	C	NC	NC
78. *T. f. fuscobalteata* (77)								NC	NC	L*	C	NC	NC
79. *T. fuscobalteata pagdeni* (77)								NC	NC	L*	C	NC	NC
80. *T. genalis* (32)					S	S		A			SC		S*
81. *T. ghilianii* (26)	–	NC	NC	NC	E	E		S	L	E	IC	1–3	S
82. *T. hockingsi* (32)	+	sev.	S		S	S		A	L	E	IC	NC	S
83. *T. iridipennis* (14, 16, 28, 32, 57, 58, 60)	–	NC	NC	NC	E	E		A,S	E,L	E	C	NC	NC
85. *T. j. jaty* (C.R., 18, 21, 29, 30)	++	2–7	S	–	E	E	–,+	A,S	E,L,S	L,s?	Co	6–24	S°
88. *T. lurida* (9, 26, 71)							+	A,U					
89. *T. mombuca* (18, 21, 42, 65)	++	7–8	S	+	L	L		R,SS	E*	L,S	SC	11	S
90. *T. nigra paupera* (C.R., 30)	–	NC	NC	NC	E	E,S	+	NC	NC	Ss	C	NC	NC
91. *T. perangulata* (C.R.)	++	1–7	H,S	–	E	E	+	A,S,U	E	L	SC	25	S
92. *T. portoi* (26)	–	NC	NC	NC				NC	NC		C	NC	NC
93. *T. sarawakensis* (77)								NC	NC		C	NC	NC

Table 4a (cont.)

	Involucrum				Pots					Brood cells			
	16. Presence	17. No. of layers	18. Rigidity	19. Merging with batumen	20. Honey	21. Pollen	22. Pollen & honey in separate clusters	23. Location	24. Shape, brood chamber	25. Shape and synchrony	26. Arrangement	27. No. of combs	28. Pillars
94. *T. silvestrii* (20, 35. 63, 65)	–	NC	NC	NC	E	L	+	NC	NC	E	C	NC	NC
95. *T. smithii* (69)	–	NC	NC	NC	E	E		NC	NC	E	C	NC	NC
96. *T. terminata* (77)	–	NC	NC	NC							SC		
97. *T. varia* (5, 36, 63)	–*	NC*	NC*	NC*	E	L		NC	NC		C	NC	NC
Trigona, s. str.													
98. *T. amalthea* (Brazil) (20, 63)					S	S			S	L	Co		S
98. *T. amalthea* (63, 70)	–	NC	NC	NC	E,S	E,S		U	S	L	Co	4,10	S
99. *T. chanchamayoensis* (63)	–*	NC*	NC*	NC*	E	E		A,U		L	BC	3–6	
100. *T. c. cilipes* (26, 63)	–	NC	NC	NC	E	E		R	E,S	L	IS	4–10	S
101. *T. corvina* (C.R., 30, 63)	+	1	S	++	E,S	E,S	–	S,SS,U	E,S	L,a	IS,$\frac{\text{SC}}{\text{Co}}$	10–30	S^{+}
104. *T. d. dimidiata* (63)									S	L	Co?	4	
105. *T. f. fulviventris* (C.R., 63)	–	NC	NC	NC	S	S		R	F	L	BC,Co	NC	L
106. *T. fulviventris guianae* (18, 21, 63)					E,S	E,S	+			L	Co	25	L
107. *T. fuscipennis* (Colombia) (54, 63)	+	1		–*	E,S	E,S	+	A,S,U	L	L	SC	35	
107. *T. fuscipennis* (C. R., 49)	–,+	1,NC	S,NC	+,NC	E,S	E,S	+	A.R,U	F	L,s?	IS	NC,18	L

	Involucrum				Pots					Brood cells			
	16. Presence	17. No. of layers	18. Rigidity	19. Merging with batumen	20. Honey	21. Pollen	22. Pollen & honey in separate clusters	23. Location	24. Shape, brood chamber	25. Shape and synchrony	26. Arrangement	27. No. of combs	28. Pillars
111. *T. nigerrima* (C.R.)	+,++	1–4	H,S	+	S	S	–	U	S	L,a	Co	12–14	S^{o}
112. *T. p. pallens* (63, 65)											Co		
113. *T. recursa* (9, 61)	–	NC	NC	NC	S	S		A	S	L	Co	7	S
114. *T. silvestriana* (C.R., 37, 63)	–,+	NC,1	H-NC	++,NC	E,S	E,S	–	S,U	E	L	Co,IS	10–19	S
115. *T. spinipes* (18, 21, 29, 63)	+	sev.		++	S	S	+		E,S	L	SC	NC–16	
DACTYLURINA													
116. *D. staudingeri* (13, 67, 68)	–,+	1	S	+	S	S		R	S	E	VC	11	S
LESTRIMELITTA													
Cleptotrigona													
117. *L. cubiceps* (45)	–	NC	NC	NC	S	S		NC	NC	E	C	NC	NC
Lestrimelitta, s. str.													
118. *L. ehrhardti* (50)	++	5–8	S*	–	E,L,S	E,L,S	NC	S	E	L	Co	12	S
119. *L. limao* (C.R., 3, 18, 21, 50)	+	1	S	+	E	E	NC	A	E	L,a	Co	30	S
MELIPONULA													
120. *M. bocandei* (44)	++	1–5			E	E	+		E		IC	NC	S

	Involucrum				Pots					Brood cells			
	16. Presence	17. No. of layers	18. Rigidity	19. Merging with batumen	20. Honey	21. Pollen	22. Pollen & honey in separate clusters	23. Location	24. Shape, brood chamber	25. Shape, and synchrony	26. Arrangement	27. No. of combs	28. Pillars
MELIPONA													
121. *N. anthidioides* (18, 21, 29)	++	2–sev.	H	–	E	E	+	U			Co	6–9	
122. *M. b. beecheii* (C.R., 2, 7, 63)	++	1–4	S	–	E,S	E,S	–,+	SS^{+}	E,S	L,s	Co	6–8	S
123. *M. compressipes manaosensis* (26)	+	1	S*	–	E	E		U	E	L	Co	10	S
124. *M. f. fasciata* (C.R.)	++	1–4	H,S	–	E	E	–,+	A,S^{+}	E	L,a	Co	8–13	S^{o}
125. *M. fasciata melanopleura* (C.R.)	++	1–6	H,S	–	E	E	+	A	E	L	Co	14	S^{o}
126. *M. f. favosa* (5)					E	E				L			
127. *M. favosa phenax* (30)													
128. *M. flavipennis* (C.R.)	++			–	E	E		S^{+}		L	Co		
129. *M. fuscata melanoventer* (9)	++	2		–						L	Co*	9	S
130. *M. interrupta grandis* (9)	++	2		–	E,S	E,S	+	S	$\frac{F}{S}$	L,a	Co	6,9	S
131. *M. interrupta triplaridis* (30)													
132. *M. marginata amazonica* (9,26)	–	NC	NC	NC	E	E		A,SS;U	S	L	Co	5–9	S
133. *M. marginata carrikeri* (C.R., 26)		1	H?	–	E	E		U	S	L	SC	5	S^{o}
134. *M. m. marginata* (3, 18, 21, 36, 56)	++	4–sev.		–	E,S	E,S	+	A,S,U	F	I	Co	1–8	

Table 4a (cont.)

	Involucrum				Pots					Brood cells			
	16. Presence	17. No. of layers	18. Rigidity	19. Merging with batumen	20. Honey	21. Pollen	22. Pollen & honey in separate clusters	23. Location	24. Shape, brood chamber	25. Shape and synchrony	26. Arrangement	27. No. of combs	28. Pillars
136. *M. nigra schencki* (3, 18, 21)	++	sev.*	H,S	–	E	E			F	L	Co	5–6	
137. *M. p. pseudocentris* (26)	++	3–4	S*	–	E	E		A	E	L	Co	10	S
140. *M. rufiventris* (18, 21)	++	sev.		–	E	E		A,SS,U	S	L	Co	15	
141. *M. santhilarii* (3, 20)	++	sev.	+	–	E	E				L	Co	5	
142. *M. scutellaris* (29, 55)	++				E	E				L	Co	4	
143. *M. seminigra abunensis* (9)	said	to agree with merrillae											
144. *M. seminigra merrillae* (26)	++			–	E	E			E*	L	Co		S
UNPLACED													
145. *T. turusiri* (22)	++	sev.			E			A,U	S	L	Co	6	

TABLE 5

Nest measurements. The column numbers refer to numbered explanatory paragraphs in the text.

Species snd references CR = treated in the section on Costa Rican nests	Entrance (mm)		Post (mm)				Brood chamber (cm)		Brood cells (mm)		Queen cocoon (mm)		
			Honey[1]		Pollen								
	1a. Length	9a. Inside diameter	20a. Diameter	20b. Length	21a. Diameter	21b. Length	24a. Diameter	24b. Length	25a. Diameter	25b. Length	25c. Diameter	25d. Length	27a. Intercomb distance (mm)
TRIGONA													
Meliplebeia													
1. *T. beccarii* (43, 68)	20–27	15–19	20–50	30–50			9–15		4	7	5	10	
2. *T. d. denoiti*, etc. (67, 68)		10	10	15			10		5		8.5	10	
3. *T. lendliana* (46)	5–10	6	20–25	25–40			6.5	6	2–2.3	4.5	4.5	7.5	2
5. *T. nebulata komiensis* (11)	6		15	15					3–4	5–6			
6. *T. tanganyikae medionigra* (46)	10–15	8–10	22–25	30–40			9–13	12	3.8–4	7			
Plebeia													
7. *T. australis* (32)	3–10	8	6–10	7–11			8	20	3.5	3.5			NC
8. *T. cincta* (32)	20–80	7–15	7–9				4.5	7	2.7	2.7			NC
9. *T. domiciliorum* (47)	25 +												NC *
10. *T. droryana* (18)	NC	2–3							2	3.5			

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(1) When sizes of honey and pollen posts are not distinguished in the original sources, the data (applicable at least in general to both kinds of pots) are recorded under honey pots only.

TABLE 5 (cont.)

	Entrance (mm)		Pots (mm)				Brood chamber (cm)		Brood cells (mm)		Queen cocoon (mm)		
			Honey		Pollen								
	1a. Length	9a. Inside diameter	20a. Diameter	20b. Lenth	21a. Diameter	21b. Length	24a. Diameter	24b. Length	25a. Diameter	25b. Length	25c. Diameter	25d. Length	27a. Intercomb distance (mm)
11. *T. emerina* (18, 21, 56)			10	14					1.75	3.5			
12 *T. frontalis* (C. R.)	NC	3	10–12	14–15			5–6	4–10	2.5	4			2.5
14. *T. molesta* (18, 21, 29)			7–13	10–18					2.0–2.6	4.0–4 2	4	6.5	2
15. *T. mosquito* (18, 21, 29)			11–14	18–20					2.0–3.5	4.5			
17. *T. q. quadripunctata* (18, 21, 29,63)	0–15	8–17	20–30	30–40			9	9	4	5			
18. *T. sp. A* (C.R.)	NC	3	8–12.5	11.5–21			12		2	4			
20. *T. schrottkyi* (18,21, 29, 36,63)	NC–3	5–10	3.5–7	3.5–7			NC	NC	2–3.5	3.2–3.5	3	5	NC
21. *T. tica* (C. R.)	NC		4	6			NC	NC	2.5	4			NC
Nogueirapis													
22. *T. mirandula* (C. R.)	10	6–8	12–15	20–30			8–16	5–13	3	4.5			2–6
Axestotrigona													
23. *T. eburnensis* (12)			15	15					3.5	6	6	9	

Table 5 (cont.)

	Entrance (mm)		Post (mm)				Brood chamber (cm)		Brood cells (mm)		Queen cocoon (mm)		
			Honey		Pollen								
	1a. Length	9a. Inside diameter	20a. Diameter	20b. Length	21a. Diameter	21b. Length	24a. Diameter	24b. Length	25a. Diameter	25b. Length	25c. Diameter	25d. Length	27a. Intercomb distance (mm)
24. *T. sawadogoi* (12)	NC	8	15	15					3.5	6	6	9	
25. *T. togoensis* (15, 44, 67, 68)	0–20	10–15	10–20	15–25			15	20	2.5–3	5–5.8		9	3–4
Hypotrigona													
26. *T. araujoi* (31, 44)	50–70	10	7	10			NC	NC			3	5	NC
27. *T. braunsi* (1, 31, 44)	20–50	3–4	5	5			NC	NC					NC
28. *T. gribodoi* (43)	6–25	3–6	6–7	6–7			NC	NC	2.2–2.3	3–3.4			NC
Trigonisca													
30. *T. buyssoni (C. R.)*	NC	2–6	5.5	15	*5.5*	*15*	NC	NC	2	3			NC
31. *T. duckei* (59)							NC	NC	1.25–1.5	2			NC
33. *T. muelleri* (19)			4.5	5			NC	NC	1.7–2.1	3.7–4			NC
34. *T. sp. B (C.R.)*	NC		7.5–13	27–30			NC	NC	2	3			NC

Table 5 (cont.)

V–4

	Entrance (mm)		Post (mm)				Brood chamber (cm)		Brood cells (mm)		Queen cocoon (mm)		
			Honey		Pollen								
	1, Length	9a. Inside diameter	20a. Diameter	20b. Lenth	21a. Diameter	21b. Length	24a. Diameter	24b. Length	25a. Diameter	25b. Length	25c. Diameter	25d. Length	27a. Intercomb distance (mm)
Scaura													
35. *T. latitarsis* (C. R., 9, 30, 63)	10–67	3.5–10	6–8	6–9			6	3–7	2–2.5	3–4			2–2.5
37. *T. tenuis* (26)	25–40	5–8											
38. *T. timida* (66)	40	6											
Partamona													
39. *T. cupira* (C. R., 18, 21, 30)	0–80	25–110	10–15	15–21			8–15	8–17	3.4–3.5	5.3–6	5.5–6	9–10	2.5–3
41. *T. testacea helleri* (18, 21, 29)		20	10–15	10–18					2.5–3.5	5.5–6.5			
42. *T. testacea musarum* (C. R.)			12–13	13–15			11.5	14	3.5	6	5.5	10	3.5
44. *T. t. testacea* (9, 26)	40–100	30–60	8–13	13–30	12	17	11–18	14–18	4	5–6			5
Paratrigona													
45. *T. guatemalensis* (C. R.)		9x21	7	10–12			8		2	3.5	3.5	7	2
46. *T. impunctata* (59, 63)									2.2	4			
49. *T. ornaticeps* (C. R.)	50	10–20	9–13	12–19	8–11	12–17	7	13	2.5	4			2–3

	Entrance (mm)		Pots (mm)				Brood chamber (cm)		Brood cells (mm)		Queen cocoon (mm)		
			Honey		Pollen								
	1a. Length	9a. Inside diameter	20a. Diameter	20b. Length	21a. Diameter	21b. Length	24a. Diameter	24b. Length	25a. Diameter	25b. Length	25c. Diameter	25d. Length	27a. Intercomb distance (mm)
50. *T. peltata pacifica* (63)							8	?	?	5		? [a]	
51. *T. p. peltata* (C. R.)	10–85	2–5 x 8–14	7–8	7–10			5–6	6–6.5	2	4	4.3	6	1.5
52. *T. subnuda* (18, 21)			15	20					2.5	4			
Scaptotrigona													
53. *T. bipunctata or postica* (18, 20, 21)	130–600	15	20–25	20–25					4	6	6.5	9	
54. *T. iheringi* (18, 21)	80	12											
55 *T. mexicana subobscuripennis* (C. R.)	10	30–45	11–18	16–25			5.5–10	7–16	2	5			3–5
56. *T. pachysoma* (30)	25–100	20											
57. *T. pectoralis* (C. R., 63)	150–1.000	4.5–5 5											
59. *T. tubiba* (18, 21)			16–18	25–30					3.5	6		10	
60. *T. xanthotricha* (9)	120	50											

(? [a]) Schearz (63) gives the length of the queen cocoon as 12 mm. This is obviously an error as the physogastric queen was only 8 mm long.

Table 5 (cont.)

	Entrance (mm)		Post (mm)				Brood chamber (cm)		Brood cells (mm)		Queen cocoon (mm)		
			Honey		Pollen								
	1a. Length	9a. Inside diameter	20a. Diameter	20b. Diameter	21a. Diameter	21b. Length	24a. Diameter	24b. Length	25a. Diameter	25b. Length	25c. Diameter	25d. Length	27a. Inter-comb distance (mm)
Nannotrigona													
61. *T. mellaria* (C. R.)	70	15					12	9	2.5	4	4	8	2.4
62. *T. testaceicornis perilampoides* (C.R., 30)	3–75	5–15	9–12	9–12			14	7		4			2.5
Cephalotrigona													
63. *T. c. capitata* (63)	NC	10	40	52									2.4
64. *T. capitata zexmeniae* (C.R., 20, 54, 63)	NC	4–12	20–45	30–55			15	25	4–4.2	6–7			
65. *T. femorata* (26)	20	8?	20	30–15			15	25	6–7	9–10			
Oxytrigona													
66. *T. obscura* (9)	NC	4–5											
67. *T. tataira mellicolor* (C.R.)	NC	4	10–15	15–20			14–16	17–26	2–3	5			3–4
68. *T. t. tataira* (29)	NC	5–7 x 40–60[1]											

[1] Slit shaped.

Table 5 (cont.)

	Entrance (mm)		Pots (mm)				Brood chamber (cm)		Brood cells (mm)		Queen cocoon (mm)		27a. Intercomb distance (mm)
			Honey		Pollen								
	1a. Length	9a. Inside diameter	20a. Diameter	20b. Lenght	21a. Diameter	21b. Length	24a. Diameter	24b. Length	25a. Diameter	25b. Length	25c. Diameter	25d. Length	
Tetragona													
70. *T. atripes collina* (69)									4.5	8			NC?
71. *T. buchwaldi* (C.R., 74)	10–50	8	9–15	35–60	10	30–50	7	9	2.5	5			2.5
72. *T. carbonaria* (32)	NC	8–16	8–23	9–20	4–6	6–10			2.4–2.6	3.7–3.8			
73. *T. clavipes* (52)			20–30	30–50			16	31					
74. *T. clypearis* (32)	6–20	10–12	5–20	7–9			NC	NC	2–2.5	2.5–3.5			NC
75. *T. dorsalis* (Central America) (C.R., 10, 30,47)	75–150	10–13	20–38	25–63			6.7–8	8–8.8	2.6	6	7	10	
75. *T. dorsalis* (Amazon) (26)	NC	6–7	18–24	25–36			9		2.6	5.5			3
75. *T. dorsalis* (S. Brazil) (18, 21)	30?	70	13–25	16–30			13	30	3–4	5.5–6	6	8–9	
76. *T. flavicornis* (26)	NC	4	5–6.5	8–30	12	20–40	NC	NC	3	5–6			NC
77. *T. freiremaiai* (35)	NC*	3	5–6	10–13	6–7	30	NC	NC	2.8–3	4–5			NC
80. *T. genalis* (32)			12–15	12–15					2.5	5			

Table 5 (cont.)

	Entrance (mm)		Pots (mm)				Brood chamber (cm)		Brood cells (mm)		Queen cocoon (mm)		
			Honey		Pollen								
	1a. Length	9a. Inside diameter	20a. Diameter	20b. Length	21a. Diameter	21b. Length	24a. Diameter	24b. Length	25a. Diameter	25b. Length	25c. Diameter	25d. Length	27a. Intercomb distance (mm)
81. *T. ghilianii* (26)	50	20	20–30	30–40			12	108	6.5–7	9–10			4–15
82. *T. hockingsi* (32)	10	17	7–12	8–13			10	37	3	4			
83. *T. iridipennis* (32, 58)	0–50	10–14	8–18[1]	10–25[1]			6–7	3–22	2.75–3	3.6–4			NC
85. *T. j. jaty* (C.R., 18, 21, 29, 30)	5–230	5–19	8–13	13–21	8–13	13–17	8–5.5	8–21	1.5–2.2	3–4.2			1.5–4
88. *T. lurida* (9, 26)	0–70	20–70											
89. *T. mombuca* (18, 21, 29, 42, 65)		4–11	10–20	40–80			10		3	7	6–6.5	8–11	3
90. *T. nigra paupera* (C. R., 30)	NC	5–8	14–15	20–33	14–15	16–33	NC	NC	3.5	4	4.5	7	NC
91. *T. perangulata* (C.R.)	NC	70	20	30	25	45	15	27	3	6			3–4
94. *T. silvestrii* (65)		2	6	8–9	6	10–35	NC	NC	3–4	5			NC
Trigona, s. str.													
98. *T. amalthea* (Brazil) (20, 63)	NC		18–22						4–7	9		13	
98. *T. amalthea* (63, 70)	60–300	40–90	12–14	15–17			14	14	5.2	8	11	14	
99. *T. chanchamayoensis* (63)	10	40	3–8	5–12									

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[1] George (17) reports that pots are 3.5–4 mm in diameter and 7–8 mm high. It is likely that he was dealing with a different species.

Table 5 (cont.)

	Entrance (mm)		Post (mm)				Brood chamber (cm)		Brood cells (mm)		Queen cocoon (mm)		
			Honey		Pollen								
	1a. Length	9a. Inside	20a. Diameter	20b. Length	21a. Diameter	21b. Length	24a. Diameter	24b. Length	25a. Diameter	25b. Length	25c. Diameter	25d. Length	27a. Intercomb distance (mm)
100. *T.c. cilipes* (26, 63)	15–182	10–14	8–9	11–12			4.5–9–7	6.5–12	3	5.2–5.5	5	6.5	3–5
101. *T. corvina* (C.R., 30)	NC	25–110	6–10	9–14	8–12	9–15	13–25	16–35	3–3.5	4.5–6	6.5–8	9–12	4–6
104. *T. d. dimidiata* (63)							11	12		9			
105. *T. f. fulviventris* (C.R., 63)	0–100	28–50	8	8	8–10	8–10	30	15	4	6–7			
106. *T. fulviventris guianae* (18, 21, 29, 63)	137.5	57	6	8–10			22		3–4	6	6	11	4–5
107. *T. fuscipennis* (54, 63)	NC	20–40	10–12	15–17					4.5	7			
107. *T. fuscipennis* (C.R.)		50	8–10	10–11	8–9	10–13			3.5	5			4–8
109. *T. h. hyalinata* (49)					12	15			4	6–7			
110. *T. hypogea* (63, 65)	NC	5	17	17									
111. *T. nigerrima* (C.R.)	35–50	20–35	10	12	11	14	13–18	12–14	4	7	8	12	4–6
112. *T. p. pallens* (30, 66)	25	25							4	6			
113. *T. recursa* (9, 63)	70	55	14	15			6	6	2.5	5.1–5.2			

	Entrance (mm)		Pots (mm)				Brood chamber (cm)		Brood cells (mm)		Queen cocoon (mm)		
			Honey		Pollen								
	1a. Length	9a. Inside diameter	20a. Diameter	20b. Length	21a. Diameter	21b. Length	24a. Diameter	24b. Length	25a. Diameter	25b. Length	25c. Diameter	25d. Length	27a. Intercomb distance (mm)
114. *T. silvestriana* (C.R.),	300	25–100	12–15	15–21			10–25	29–32	4.5	6	10–12	13–15	5–6
115. *T. spinipes* (18, 21, 29, 63, 65)	NC		10–15	12–15			7.5–20	10–20	3–4	5–6.3	8–9	11–12	6–8
DACTYLURINA													
116. *D. staudingeri* (13, 68)	NC	70–100	10–12	10–12					2	3	5. 5	7- 8	
LESTRIMELITTA													
Cleptotrigona													
117. *L. cubiceps* (45)	50	4	5	6			NC	NC	2.5 - 3.5	3.5 - 4	3.5	4.5	NC
Lestrimelitta, s. str.													
118. *L. ehrhardti* (50)	110	20	10–30	30–50			8	9	3.5	6–6.5			1.5–2
119. *L. limao* (C.R., 50, 63)	160–600	5–16	12–19	30–32			23	29	3	5	5	7	
MELIPONULA													
120. *M. bocandei* (44)	NC	5x25	22	30–35			15–18	20–25					

Table 5 (cont.)

	Entrance (mm)		Pots (mm)				Brood chamber (cm)		Brood cells (mm)		Queen cocoon (mm)		
			Honey		Pollen								
	1a. Length	9a. Inside diameter	20a. Diameter	20b. Length	21a. Diameter	21b. Length	24a. Diameter	24b. Length	25a. Diameter	25b. Length	25c. Diameter	25d. Length	27a. Intercomb distance (mm)
MELIPONA													
121. *M. anthidioides* (18, 21, 29)	NC	8–9	25–30	31–50					5–6	8–10	NC	NC	7
122. *M. b. beecheii* (C.R., 2)	NC	8	25–38	28–38			8–18	8–15	5	9	NC	NC	6
123. *M. compressipes manaosensis* (26)		8–9	12–31	20–35			8	12			NC	NC	
124. *M. f. fasciata* (C.R.)	NC	7	20–30	30–55			10–12	20–22	4–5	10	NC	NC	5–7
125. *M. fasciata melanopleura* (C.R.)	NC	8–9	30–40	40–60			10	20	5	9	NC	NC	6
126. *M. f. favosa* (5)				37–50					5	8	NC	NC	
127. *M. favosa phenax*	NC	6–7									NC	NC	
129. *M. fuscata melanoventer* (9)	NC	8	30	50			11		5.5	10.5	NC	NC	
130. *M. interrupta grandis* (9)	*NC*	14	30–40	40–50			16	13	6	13	NC	NC	
131. *M. interrupta triplaridis* (30)	NC	12									NC	NC	
132. *M. marginata amazonica* (9)			19–25	25–35			5	4	3.5–4	7–8	NC	NC	4

Table 5 (cont.)

	Entrance (mm)		Pots (mm)				Brood chamber (cm)		Brood cells (mm)		Queen cocoon (mm)		
			Honey		Pollen								
	1a. Length	9a. Inside diametre	20a. Diameter	20b. Length	21a. Diameter	21b. Length	24a. Diameter	24b. Length	25a. Diameter	25b. Length	25c. Diameter	25d. Length	27a. Intercomb distance (mm)
133. *M. marginata carrikeri* (26)	NC	4–4.5	25	30			7	6	4	9	NC	NC	
134. *M. m. marginata* (18, 21, 29)	NC	4.5	13–31	13–46			6.5		3.5–4.5	6–8	NC	NC	
136. *M. nigra schenckl* (18, 21, 29)	NC	6–7	20–60	25–80			10	6	5	8.75–10	NC	NC	5
137. *M. p. pseudocentris* (26)	NC	7.5	30–40	42–48			14	23	4.1–4.2	6.2–6.4	NC	NC	
140. *M. rufiventris* (18, 21, 29)	NC	8–15	35–40	45					4–5.5	10–11	NC	NC	7–8
141. *M. santhilarii* (3, 20)	10	10	15–17	30–35					4–5	10	NC	NC	5
142. *M. scutellaris* (29, 55)	NC–130	9–10	25–55	40–75					4.5–6	10–12	NC	NC	
143. *M. seminigra abunensis* (9)	50	45	48	55							NC	NC	
144. *M. seminigra merrillae* (26)	20–28	40–50			23	34					NC	NC	
UNPLACED													
145. *T. turusiri* (22)	NC		30	40					4	8			

Nest structures should be observed in the field to understand their environmental relevance. Thousands of angry bees do not help to do this well, nor does the complexity and perishability of the nests. Being full of honey, larval bees, and waxes which soften with heat and dissolve in many solvents (including some that may be used to kill bees), preservation of nests for subsequent study is usually impractical. Moreover, they are often in heavy logs. Our methods have included felling of trees, use of axes, saws, crow bars, shovels and picks to get at the nests, and descriptions, sketches, and photographs for recording the data. Obviously others have done likewise, and the result is a surprisingly extensive body of information. Yet it is often deficient in data that must have been known to or easily obtainable by the observer when he opened a nest. We hope that one function of this paper will be to encourage the more systematic collecting of such data in the future.

In the tables the columns are numbered for ready reference, those in Table 5 being associated by number with related columns in Table 4. The species are also numbered in these and other tables for ready comparison among tables.

Subspecific names are utilized freely. In most groups this procedure would not be needed but in Meliponinae, due to the conservative approach of Schwarz, many of the American forms called subspecies (= varieties by Schwarz) are turning out to be specifically distinct. In the absence of further studies it is not possible to say, in a given instance, whether forms distinguished by trinomials are specifically different or not. In order not to mix information, we keep the trinomials for the present, except in cases where they have been raised to specific rank in previous publications. In a few cases the architectural information suggests the existence of cryptic species and the data are therefore kept separate in the tables. For example, two different types of nests are recorded for *T. fuscipennis*. We suspect that two species are involved and have provided a line for each in the tables.

In some cases there are problems with regard to identifications by earlier authors. Many of these are discussed in detail by **Schwarz** (63). When identifications seem uncertain we have chosen to ignore data provided by earlier authors rather than risk confusion.

2. **Symbols used in the tables**: The following paragraphs, numbered to correspond to the columns of Tables 4 and 5, explain the symbols used in these tables:

NC (no comparison) is used for logical impossibilities. For example, if there is no entrance tube it is impossible to state whether or not it is perforated. An asterisk (*) following a symbol shows that while the condition was not precisely stated in descriptions, it is inferred from lack of comment or from other items described. To indicate a condition between two alternatives, one symbol is placed above another (e.g., $\frac{+}{-}$ or $\frac{s}{u}$). Variation is indicated by showing a range (1–3) or two conditions separated by a comma (–, +).

1. **Length of external entrance tube:** In Table 4, ++ = longer than wide; + = as long as or shorter than width; – = absent as a projection beyond the surface of the substrate. Of course for all nonexposed nests, the entrance tube extends through the substrate —ground or wood— from the nest to the surface of the substrate. This

distance is not considered in the tables. In Table 5 the length of the tube is showr in millimeters. When the sides of a tube differ in length, an average is given; NC is for those lacking an external tube.

2. **Shape of external entrance tube:** F = funnel–shaped; C = cylindrical; T = tapering toward the apex; I = irregular; NC for those without external tubes. In some cases an entrance that does not project is not marked NC, usually because of a funnel shape, F.

3. **Rigidity of entrance tube:** H = hard; F = firm but not brittle; S = soft, at least at apex; NC for those without external tubes. Occasionally rigidity is indicated for cerumen at the entrance even though not projecting as a tube.

4. **Ornamentation of entrance tube:** This column is used to record the curious projections and excresences that occur on entrance tubes of some species, L = large projections; E = earlike projections around entrance (possibly as much related to the funnel–shaped expansions of the entrance [*2 above*] as to projections along the tube); S = slender or rootlike projections; A = ornamentation absent; NC for those without external tubes.

5. **Perforations of entrance tube:** ++ = numerous and distinct; + = present but few, often present only near extreme apex of tube; – = absent; NC for those without external tubes.

6. **Tube lip:** C = margin of opening thick and crenulate; T = not crenulate but thick; Th = margin thin (less than 1 mm.), often delicate, sometimes irregular but not regularly crenulate; NC for those without external tubes.

7. **Night closure:** + = entrance closed (although closure usually or always perforated) at night; – = entrance tube open at night, as in the daytime.

8. **Radiating ridges around entrance:** ++ = strong; + = weakly developed; – = ridges absent. Such ridges occur in forms usually without projecting entrance tubes and are in hard material (mud) immediately around the entrance, including the material used to reduce the size of the original opening of the nesting cavity.

9. **Size of the entrance:** In Table 4, ++ = many bees in the entrance at the same time or entrance large enough for many; + = 2–4 bees; – = one bee and entrance so small that one bee blocks it. The entrance diameter shown in Table 5 is so far as possible the inside diameter at the apex of the tube, if any, including the full flare of funnel–shaped entrances. In some cases the literature does not say how measurements were made; we are therefore unable to be certain that all measurements quoted were made in the way indicated.

10. **Sometimes with two or more entrances:** + = yes; – = no. No species always has multiple entrances.

11. **Internal entrance tube:** ++ complete; + = partially developed; –, absent. This does not concern the tube passing through the substrate. The internal tube is the continuation of the entrance into the nest proper. When complete it usually ends near food pots.

12. **Number of layers of batumen:** This is given as numbers, except when literature is indefinite, when we use sev. = "several" and few = "few"; irrg. = irregular layers so that the number is difficult to count. NC is used for those lacking batumen. The number 1 ordinarily means that there is a lining batumen and batumen plates only, although a single thick batumen layer encloses some exposed *Paratrigona* nests. Larger numbers indicate at least some lamination of the batumen, with an outer layer ordinarily lining the nest cavity when the nest is in a cavity.

13. **Lining batumen:** ++= strong: + = thin; ± = an incomplete lining; – = absent. NC for exposed nests and nests with laminate batumen, whether exposed or in cavities. The outer layer of laminate batumen, even if applied to the inner surface of a nest cavity, is not counted as lining batumen for this purpose.

14. **Batumen plates:** M = made of mud and presumably resin (perforated in *Melipona*); C =made of cerumen;– = plates lacking even when the cavity space is so extensive that it would ordinarily be limited by plates; NC for exposed nests and for enclosed nests that occur in cavities that need no shortening by plates, e.g., spherical cavities in soil, termite nests, etc.

15. **Plant or fecal material or mud in outer layers of batumen:** + = distinct; – = not obvious. (This is an attribute of some exposed nests only and NC is used for those in cavities.)

16. **Involucrum:** ++ = conspicuous and continuous; + = discontinuous; – = absent.

17. **Number of layers of involucrum:** This is given as numbers, except when literature is indefinite when we use sev. = "several" and many = "many"; NC for those lacking involucra.

18. **Rigidity of involucrum:** H = hard; S = soft; NC for those lacking involucra.

19. **Involucrum merging with batumen:** ++ = merging; + = slightly merging; – = involucrum and batumen fully distinct. In forms with laminate enveloping sheets there may be every intergradation between involucrum and batumen (++, +), the pots sometimes being scattered and not providing a clear separation. Texture is not a guide. The outer enveloping sheets are usually hard, the inner ones soft, but there is often every gradation and the transition may not correspond to the location of the pots. The inner layers of batumen may be soft or the outer layers or even most of the involucrum may be hard. On the contrary, in many forms (–), batumen and invlucrum are fully separated in position, texture, and color. NC for those lacking involucra.

20. Shape of honey pots: In Table 4, S = subspherical; E = oval; L = elongate, over twice as high as wide. Because they are usually pressed together in groups, they are usually angular and the shapes indicated are only approximations. In Table 5 measurements of pots are given to show ranges of size for each species. Pollen pots are the same size as honey pots in most species and observers have commonly recorded the data with no distinction between the kinds of pots. Measurements in columns 20a and b, Table 5, when not associated with data in columns 21a and b, refer therefore to pots of either or both kind. Measurements of honey pots proper are found in columns 20a and b when associated with data on pollen pots in columns 21a and b.

21. Shape of pollen pots: Symbols and explanation as for 20.

22. Segregation of honey and pollen pots: ++ = in separate chambers; + = in partially separated clusters but with contact or limited intermixture; – = fully intermixed. It is likely that the distinction between + and – is largely an artifact; NC for *Lestrimelitta* in which honey and pollen are mixed in each pot. Both materials are occasionally found in a single pot of other species but usually honey is on top of pollen with essentially no mixture.

23. Positions of pots in relation to the brood chamber: A = above; U = below; S = at the side; SS = on two or more sides; R = all around, i.e., above, below, and on the sides; NC for those with dispersed brood, i.e., those lacking distinct brood chambers. A plus (+) marks conditions likely to result from unusual nest sites, e.g., horizontal rather than vertical nest cavities. In a horizontal cavity, pots are often by necessity at the sides rather than above or below the brood chamber.

24. Shape of the brood chamber: For Table 4, L = elongate (height twice the diameter or more; E = oval; S = subspherical; F = flattened, i.e., much broader than height; NC for those with dispersed brood, i.e., those lacking brood chambers. In Table 5, dimensions of brood chambers are given. Median horizontal diameters of brood chambers are typically more or less equal but when unequal due to flattening of a nest by a cavity or against a tree (in the case of exposed nests), an average diameter is given; NC as for Table 4

25. Shape of brood cells: For Table 4, S = spherical; Ss = subspherical, usually an occasional cell spherical; E = oval; L = elongate, i.e. with parallel sides due to crowding. For Table 5, dimensions are given, both for ordinary brood cells and for queen cocoons; NC for queen cocoons of *Melipona* which are the same size as other cocoons. The accuracy of available measurements (usually only to one half mm) is such that a size distinction between cells and cocoons of ordinary brood is not practical. Species with spherical cells have oval cocoons; in these cases measurements are based on cells. Probably many of the other measurements in columns 25a and b, Table 5, are based on cocoons rather than cells. An "a" means that cells are produced asynchronously, "s," sychronously, as inferred from similarity or dissimilarity of new cells in nests at the time of opening them.

26. Arrangement of brood cells: C = in unstructured clusters; CL = in concentric layers; IC = in irregular combs, i.e., intermediate between clusters and combs; BC = in irregular combs but not suggestive of clusters; Co = in combs; IS, in irregular spiral combs; SC = in spiral combs; VC = in vertical combs.

27. Number of combs: This information is provided as a range for each species. In the very few recorded cases where a single nest contained multiple and wholly isolated brood chambers, the figures given are for the separate brood chambers and not for the total number of combs in the nest; NC for those with cell arangements (item 26) C, CL, and for the more irregular arrangements included under IC and IS, where counting is not meaningful.]

28. Pillars in the brood chamber: S = short, between individual combs; L = long, extending through several combs, not straight; LL = long, straight, extending through several combs and often through sheets of involucrum; NC for those without combs, i.e., C, Cl, and for the most irregular IC and IS categories of item 26. A small circle following an S means that the number of short pillars is reduced, sometimes to zero, among combs of cocoons while a + means that there are as many such pillars between combs of cocoons as between combs of cells.

C.— **Nest Entrances.**

For most meliponine nests, one sees no more than the entrance without digging in the ground or cutting and splitting trees. The entrance is of considerable biological importance to judge by its interspecific diversity.

1. **Lack of an external entrance tube:** Even when there is no external tube, the entrance is more than a mere passage into the nesting cavity. Whatever natural passageway exists is narrowed to a size appropriate for the particular species of bee by means of cerumen or sometimes (e.g., *Melipona*) mud mixed with cerumen or resin. This is the external end of the lining of the tube through the substrate (except for exposed nests). Even in the numerous species with no projecting external entrance tubes (– in column 1, Table 4), there is usually considerable material placed around the opening by the bees. An exception is in *T. tica* which utilizes such tiny holes that there is no need for much propolis to narrow the entrance. (fig. 23). The surface of the entrance material may be depressed or flush with the surface of the substrate, or may project slightly as a rim or feeble mound around the entrance holes. The material may spread out over the surface around the entrance. Thus, in *T. carbonaria* and to a slight degree in *T. nigra paupera* there is often hard, black material spread onto the surface of the tree trunk or other substrate around the entrance (fig. 2).

The surface of the material around the entrance may be smooth (as in *T. carbonaria*) or slightly roughened as in *T. capitata zexmeniae* and Mesoamerican *Melipona*. On the other hand, in the South American *Melipona* (except *seminigra* which has a specialized entrance) the mud (hardened by resin?) around the entrance is usually formed into conspicuous radiating ridges (Fig. 3). This feature is

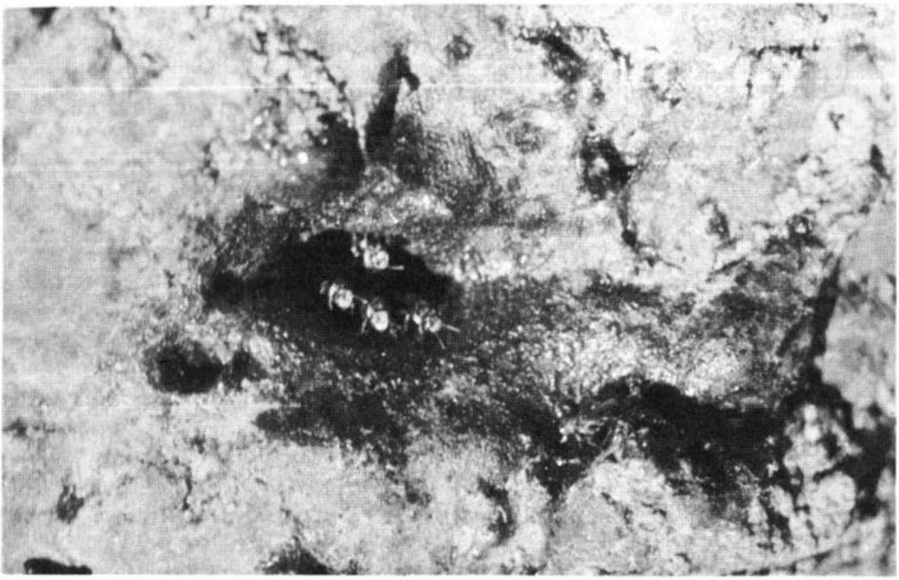

Figure 2. Nest entrance of *Trigona (Tetragona) carbonaria* (*sp.* 72).

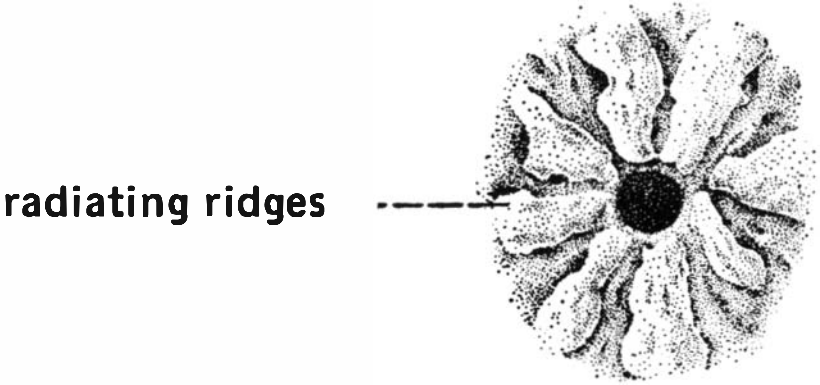

Figure 3. Nest entrance of *Melipona* (from *Kerr* et al., 26).

so consistent that South American authors have sometimes regarded it as a character of the genus. Yet not one of the Mesoamerican species makes such ridges.[1] *M. marginata* occurs in both areas, but the subspecies from both southern Brazil and the Amazon make radiating ridges while that from Costa Rica does not. Thus it is not as though there were different groups of *Melipona* in the two areas, but rather there must be some environmental factors influencing populations of all species or groups to make such radii in South America and not to do so in Mesoamerica. Somewhat similar but weak radiating ridges of the cerumen around the nest entrance are known in *T. flavicornis* but not in other Meliponini.

2. **External entrance tubes and defense:** As shown in Table 4, most Meliponini, unlike those discussed above, have entrance tubes that project from the substrate, or from the nest surface in the case of exposed nests. Such entrance tubes are made of soft or hard cerumen, sometimes strengthened with mud, feces, or leaf material or even consisting of mud and sand.

Entrance tubes usually project horizontally or nearly so, and little water would be taken in by them in rain storms. However, tubes of subterranean nests project straight up, chimney-like, and occasional nests of other species do the same (e.g. one out of 49 nests of *T. testaceicornis perilampoides,* **Michener,** 30). Apparently the amount of water that enters a nest via the open entrance, even if facing upward, is not a serious factor.

Entrance tubes have a variety of features, the adaptive significance of some of which can be understood.

Probably all external entrance tubes have the effect of reducing the likelihood that intruders such as other insects or spiders will wander into the bees' nest. As shown in column 7, Table 4, this danger as well as that from specific parasites or predators that might search out nests is further reduced by the habit of closing the entrance at night. This occurs in various unrelated species. The closure is made with soft cerumen from around the entrance, usually at the apex of the entrance tube (fig. 73), but *T. tica* closes the entrance in the same way even though it has no projecting tube. Species in the south temperate region (e.g., *T. australis* in Australia) may leave the opening closed for days at a time in cold weather. The closure is always perforated by small holes (for ventilation?).

A further method of excluding wanderers or enemies has been noted for a few species. It consists of placing small bits of very sticky resin on the outside of the external entrance tube. We have noted this especially in the case of *T. peltata peltata,* a species that often nests in ants' nests, and we have seen ants entangled in this material. Nests made without ants (or more probably, bee nests surviving after the demise or departure of the ants) lack the sticky material on the tube. See also notes on *T. jaty* under H, Costa Rican nests.

The size of the opening is also probably related to defense, whether or not there is a projecting tube. Columns 9 and 9a, Tables 4 and 5, show something of the variation in the size of the opening. For some species it is large (fig. 71) so that

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[1] It should be noted that our observations were mostly made before either of us recognized the interesting problem of radiating ridges. We would not have failed to see strong ones such as are found in South America but might have missed weak ones. We recently examined an entrance of *M. favosa phenax* in Panama which had two weak radiating ridges but they looked as much like accidents as normal construction (fig. 3a).

numerous bees can come or go at the same time, and the entrance in such cases is usually more or less lined with bees facing outward. Nearly all of the highly aggressive species have such entrances, perhaps to facilitate the prompt egress of alarmed bees. However, some gentle species such as *T. testaceicornis perilampoides* and *T. fulviventris* also have such entrances. Many species have somewhat smaller entrances (fig. 86), able to accomodate only a few bees at a time. Guarding is often not obvious in such cases but some of these species are aggressive, e.g., *T. guatemalensis*. Entrances which ordinarily accomodate only a single bee, although they are large enough to contain more, include *Trigona nigra paupera* (figs. 101, 101a). A few *Trigona* and most *Melipona* have small entrances through which only a single bee can pass at a time (fig. 3a). In these cases a bee, blocking the entrance with its head, can be called a guard. Effectiveness of such guards is not known but they seem timid for they withdraw into the nest at any disturbance. Perhaps they are effective against certain enemies. Most of these species are not or scarcely aggressive. The famous fire bees, the highly aggressive *T. tataira* and its relatives of the subgenus *Oxytrigona*, however, have small although usually slit-shaped nest entrances.

A pattern that permits a number of bees to rest at or guard the entrance, yet does not present a wide open hole to the attack of enemies, would seem desirable. Funnel–shaped entrances accomplish this for the throat can be relatively narrow while the flaring sides provide space for bees. Flattened or slit–shaped entrances may have the same function. Most entrances are more or less round in cross section but those of *T. p. peltata* and *T. guatemalensis* are usually vertically compressed, while those of *T. tataira* are vertical slits. **Wheeler** (71) reproduces an illustration of a curiously funnel–shaped and laterally compressed nest entrance of an Indian *Trigona* and C.D.M. has seen similar entrances made by *T. apicalis* in Malaysia. (CMD has seen an entrance of *T. t. perilampoides* much narrowed because of the little space between two rocks in a wall where it was located. Entrances of nests of this species are typically round.)

In the subgenus *Partamona* there usually exists a laberynth (fig. 39) inside the nest entrance. It is either in the substrate or, if the nest is exposed, in a projection from the side of the nest with the entrance at its end. In *T. testaceicornis perilampoides*, *Lestrimelitta limao*, and a few others, the entrance, at the base of the tube or in the substrate, may be full of coarse pillars and connectives (figs. 75, 76). The same is true of the entrance of *T. sp. A* although there is no external tube. In *T. corvina* and *Dactylurina staudingeri*, both species with exposed nests, the entrances are areas without batumen sheets and with rods and sheets parallel to the axis of the entrance. The meaning of these complications inside the nest entrances, so different from most nests which have a clean open entrance tube, is not known and may not be the same in each species. They could serve to confuse enemies. Possibly a more likely explanation, except for the gentle *T. t. perilampoides* and *sp. A*, is that the surfaces provide resting places for large numbers of bees whose attacks can be quickly released by the alarm pheromone or some other stimulus.

Some of the external structures at nest entrances may help to render the entrance cryptic. Thus AW observed that the earlike projection at the entrance of *T. perangulata* so resembled small fungi growing on tree trunks that the entrance proper was not easily seen. The slender rootlike projections on the entrance tube of *T. dorsalis* (fig. 82) also tend to make the entrance unrecognizable in a moist

Figure 3a. *Melipona favosa phenax* (*sp.* 127), nest entrance, from walls of Old Panama, Panama, showing vague radiating ridges of mud.

3a

forest full of aerial rootlets. Many of the other "ornaments" on entrance tubes (fig. 142) have no functions apparent to us. Perhaps the sloping external laminae on the mature tube of *T. cilipes cilipes* serve to drain off rainwater under wet forest conditions.

3. **Recognition as a function of distinctive entrances:** While entrance tubes probably have defense functions as indicated above, they probably also serve in many cases to make the nest entrance conspicuous and easy to find and enter for the bees. Such a recognizable entrance should speed their return after foraging, facilitate learning the location, and thus reduce time needed for orientation flights. This view may seem unlikely in view of the rapid flights to and fro from even the most inconspicuous entrance. However, the importance of the entrance tube is indicated by the fact that it is commonly the first structure made at a new nest site. *T. latitarsis,* as already noted, makes a tube on the outside of an intact termite nest before beginning to make a cavity. New nests, as yet with no combs and no queen, normally have well–formed entrances as shown by nests of *Melipona marginata amazonica* and *Trigona cilipes cilipes* described by **Kerr** *et al.* (26). Moreover, when *Lestrimelitta limao* invades another nest, it starts promptly to construct its distinctive entrance tube (**Sakagami** and **Laroca,** 50). Hence it is a reasonable surmise that the entrance structure and color provide important cues for bees returning to a nest. There is likely to be an evolutionary compromise between making the nest entrance conspicuous to help returning bees and incospicuous to hinder enemies. The following paragraphs concern some features which make nest entrances conspicuous to us.

Funnel–shaped entrances (figs. 37, 38, 64, 65) are enlarged apically and the enlargement can scarcely be protective unless merely by providing space from which bees can take off for an attack. Such an explanation would hardly serve for *T. fulviventris fulviventris* which is not aggressive. The funnel serves as a landing platform for returning workers, which therefore may be able to enter the nest with less delay than if they had to fly to a cylindrical tube, one after another. The funnel allows several to get in simultaneously. The ear–shaped structure on a few nest entrances may also provide a landing platform; behavioral observations of such entrances are needed.

Fanning bees may line a funnel; this is especially noticeable for *T. fulviventris fulviventris.* Thus another function of a funnel–shaped entrance may be to provide space for such fanning, which presumably is related to temperature control. Species without funnels, even *Melipona* with its small nest entrances, also fan, sometimes inside of the external entrance tube but also inside the nest.

The length of the entrance tube varies (figs. 71, 74, 142) from a few millimeters to a meter (estimated length of a downward slanting tube of *T. pectoralis* too high in a tree for direct measurement, Coto Brus valley, Costa Rica). Some species consistently make rather short tubes, others longer ones, as indicated in columns 1 and 1a, Tables 4 and 5. It does not seem likely that a long tube can be more effective in defense than one of moderate length, and a long tube is more conspicuous.

The apical part of the tube is often whitish or yellowish (e.g., *T. jaty jaty,* (fig. 87) and therefore relatively conspicuous. According to Nogueira–Neto (in

Michener, 32), the apex of such a tube may be of pure wax, the only place where wax without an admixture of propolis is used in meliponine construction. The tubes which readily melt in the sun (see below) are entirely pale and perhaps consist of pure wax.

The material from which projecting entrance tubes are made is usually cerumen, often hard, sometimes also brittle, often firm but slightly flexible, and sometimes soft. The apical part of a tube is typically softer than the base. Of course softness varies with temperature and external entrance tubes of subterranean species, on soil exposed to the sun, are known to melt down both in Costa Rica and the Transvaal. In the former country the species concerned (*T. mirandula* and *buchwaldi*) normally nest in shaded forest soils and the entrances do not melt except after clearing, but in the bush and savanna country of South Africa nests may be normally in the open.

Entrance tubes, however, sometimes contain foreign materials which make them recognizable and are perhaps important strengthening substances. Thus entrances of *T. cupira* and *T. testacea* subsp. look as though they contain mud in addition to propolis or cerumen and we have never seen them soft, much less melted, even though they are sometimes in the sun. The entrance tube of *T. lurida* is also reported to contain mud. Entrance tubes of the subterranean *T. quadripunctata* subsp. and of the species identified by **Ihering** (20) and **Bertoni** (3) as *Melipona santhilarii* consist of mud, mixed with sand in those of the latter. Tubes of *T. apicalis apicalis* and *T. atripes collina* are said to have sand particles embedded in the cerumen.

Because of the attributes discussed above, nest entrances of most species are recognizably different from those of others, in spite of the great plasticity related to the nest site. It is likely that such specific differences are selectively important. Workers will be less likely to mistake a nest of a different species for their own. Far more important, a young queen, on flying toward a newly prepared nest site or on returning from her mating flight, should be less likely to blunder into a nest of a foreign species and be killed. Such queens are inexperienced as field bees and if equipped to recognize their own kinds of nest entrances, and to avoid others, their survival should be enhanced.

Although entrances have distinctive features of color, texture, and form, enormous intraspecific variation sometimes occurs. For example, while one of us (**Michener,** 30) found entrance tubes of 52 nests of *T. t. perilampoides,* 49 of them in the ruins of Old Panama, to vary in length from 3 to 20 mm, a visit to the same place in 1970 revealed, in addition to entrances of the usual sort, one entrance tube of 75 mm and another 150 mm long, thus suggesting the related *T. mellaria* as found in Costa Rica.

D.— **Drainage tubes**

Nests in the soil often have a more or less vertical, lined or unlined tube (fig. 26) extending straight downward from the bottom of the nest. Such tubes, roughly the diameter of entrance tubes, are believed to drain away excess water. Drainage tubes of this type are known in nests of *T. tanganyikae medionigra, T. lendliana* (not all nests), *T. denoiti, T. testacea testacea,* and *T. mirandula* (not all nests). In the case of *T. t. medionigra,* such a burrow was 95 cm deep. In *T. beccarii* a similar tube extends down from a sharp bend in the entrance burrow rather than from the nest itself. *T. mirandula* may have up to three short tubes (lined) instead of one long one. In *T. buchwaldi,* several small unlined places in the bottom of the nest seem to take the place of the drainage tubes of the species listed above.

T. mombuca, another subterranean species, suspends its nests in the upper parts of abandoned chambers of leaf cutter ants. Since the bee nest is considerably smaller than the chamber, there is space for excess water in the latter below the nest and no drainage burrow is dug.

It seems nearly certain that the drainage burrows described above were dug by the bees. Therefore subterranean cavities themselves might sometimes be excavated or modified by bees, although the view expressed earlier that the bees merely appropriate cavities of other organisms (ants, termites, small mammals) is generally acceptable.

E.— **Protective layers.**

As indicated in discussing nest locations above, an important part of the protection of unexposed nests from varying temperature, and also from flooding, battering by rain, and attacks of enemies too large to pass through the entrance, is provided by the substrate—soil or wood. Nests of some minute species, principally of the subgenus *Trigonisca*, do not add protective layers so far as we know. However, nearly all other forms add at least one layer of cerumen to the walls of the nest cavity. This is the batumen.

1. **Batumen in nest cavities:** When there is only one layer of batumen, it probably is not important in temperature control but may waterproof the nest cavity and thus exclude excess water in the substrate. It may also be important in controlling fungal growth in the nest cavity. Antibiotic properties of propolis collected by honeybees are well known (**Lavie,** 27 and it seems likely that propolis collected in the tropics by Meliponini has similar properties. The batumen also closes off portions of a tree cavity too large for the requirements of the nest. Such a single layer (Table 4, colum 12) consists of (a) lining batumen covering the inner walls of the nest cavity and (b) thick batumen plates cutting off parts of a cavity.

The batumen plates are absent if the cavity is naturally of the correct size. However, since most tree cavities are elongate, they are commonly reduced to apropriate proportions by plates across the cavity above, below, or both above and below the nest (figs. 88, 89). Batumen plates may also be constructed lateral to the nest in a horizontal cavity or may close off a lateral branch cavity. Probably all species that typically make such plates may omit one or both (or all) of them in cavities of the proper size and form. Since cavities in the ground are normally more or less spherical and not elongate like tree cavities, batumen plates are not constructed by subterranean species except perhaps in unusual or artificial sites. Batumen plates are usually dark in color and made of very firm but not or only slightly brittle cerumen. They are usually the strongest constructed parts of a nest. They may be thin but range up to 12 cm in thickness (*Melipona rufiventris,* **Ihering,** 18, 21). In a few species of *Trigona* and in all *Melipona* they contain mud in addition to cerumen, and in the latter genus they have numerous fine perforations (fig. 147) which serve for ventilation (**Nogueira–Neto,** 38). Occasionally there are two or three batumen plates in close succession as though the bees, after making one, constructed another to further restrict the nest space.

The lining batumen consists of a layer of cerumen (sometimes with clay and sand grains in *Melipona,* e.g., *M. marginata marginata,* **Ihering,** 18, 21) which lines the nest cavity. Almost always it is plastered against the wall of the cavity regardless of irregularities in the latter, and it is continuous with but much thinner than any batumen plates that are present. In thickness, lining batumen in tree cavities varies from a barely perceptible film to a layer two or more millimeters thick. Occasionally it only partly covers the inner wall of the nest cavity, but this situation may well characterize only young nests. On the other hand, the lining batumen of subterranean nests, both in America and Africa, is commonly 1 to 5 mm thick and so strong that the whole nest can be excavated and moved about without breaking the batumen.

In nests of some species located in cavities, the batumen is laminate, i.e., made up of several layers of cerumen with spaces in which bees can commonly be found between the layers (figs. 39, 40). There are holes through the sheets, or they are incomplete, allowing access to the interlaminar spaces. The outer layer may be exactly like lining batumen and batumen plates, but the other layers are supported by pillars or points of contact with the outer layer and plates, and not constructed against any surface. Commonly the number of layers in laminate batumen varies from one part of a nest to another. Part of the variation listed in Table 4, column 12, is due to variation within nests, the rest to variation among nests. Often (e.g., fig. 62) the layers are so interrelated as to form many cellular spaces and it becomes difficult or impossible to follow any one layer or to count the number of layers with any satisfaction. As shown in the table, however, laminate batumen is uncommon for species nesting in cavities, and is quite variable in its occurrence even among species that sometimes have it. Thus for certain species (e.g., *T. carbonaria*), different nests vary from having only a single batumen layer (lining plus plates) to having multiple layers.

2. **Batumen of exposed nests and the "scutellum"**: Some forms with exposed or partially exposed nests do not have laminate batumen. Nests of *T. peltata peltata* either originally or by loss of surrounding leaf covers and ant nests are sometimes exposed; the batumen is of only one layer, less than one mm thick (fig. 59). The only known nest of *T. guatemalensis* was also exposed. The batumen was thicker, 10 to 15 mm. While not called laminate, it had cavities and spaces in it (fig. 50), so that it might have been considered laminate with the sheets and connections thickened until the spaces between were reduced. The nests of *T. peltata* and *guatemalensis* were all in relatively shady situations. The batumens were strong but probably of little effectiveness in temperature control.

Partially exposed nests such as most of those of *Partamona* and fully exposed nests such as those of various species of the subgenus *Trigona* have laminate batumen, as shown in column 12, Table 4 figs. 39–41, 119, 136. Sometimes parts of nests of *Partamona* have only a single batumen layer, but the batumen is typically laminate. One can occasionally see a single batumen layer, which by itself would have to be called a thick lining batumen, splitting as one progresses around the nest into several layers. No *Partamona* nest, however, is without multiple layers in some areas and most have them throughout.

In the fully exposed nests the layers of batumen are numerous and mostly strong, of firm and sometimes brittle cerumen. The whole nest can be buffeted by storms and can even fall to the ground from high trees without breaking to pieces in the case of *T. corvina*. The strong batumen layers hold it together and colonies may survive for some time in nests that have fallen. Hard work with a hatchet or machete is needed to get into the strongest nests, such as those of *T. corvina* and *spinipes*, when the earthen deposits described below are well developed. The outer layer, however, is commonly thin and delicate or brittle. Therefore if a person or vertebrate predator touches the outside of the nest, the outer batumen is broken and the aggressive bees swarm out. In some nests of *T. corvina*, the outer layer, so far as we can see, may be made of cerumen but it may also contain plant fibers gathered from animal droppings. In some other species the outer layer contains much chewed green leaf material (*T. amalthea*), plant fibers extracted from the dung of herbivorous animals such as cattle and horses (*T. spinipes, corvina*), or feces of animals (*T. nigerrima*). In some cases (*T. amalthea*), several outer layers are built of such material. In *T. spinipes* the layers have a median lamella of vegetable fibers (**Nogueira–Neto,** 39) but they are so covered with cerumen that the vegetable material is not easily recognizable.

The enveloping sheets, together with the spaces between them in exposed nests, may achieve impressive thicknesses, e.g., 9 cm for *D. staudingeri,* or 31 cm at the top of a large nest of *T. corvina* (fig. 114). These measurements include not only the air spaces between the sheets but the earthen "material" found in nests of *T. corvina,* etc.

In exposed nests there are sometimes supernumerary openings probably for ventilation and temperature control. Fanning by bees produces the air currents. *T. corvina* and *spinipes* occasionally have a secondary opening in the nest wall. In *T. staudingeri* there is sometimes an entrance–like opening on the side opposite the entrance. There are also small openings made in the outer layer of the batumen (13). Opening and closing of both types of openings is supposed to be related to temperature, although the evidence for this relationship is not shown decisively by the published accounts.

Much additional work on temperature control and its mecahinsms in meliponine nests is needed but at least it seems likely that the openings discussed above provide one of the mechanisms.

In exposed nests waste material plus material brought into the nest often accumulate on and between the layers of batumen. **Nogueira–Neto** (39) identified dead bees, cocoon fragments, vegetable fibers, sand, clay, propolis, etc., in such earthen material from nests of *T. spinipes.* Sometimes the material merely thickens the batumen layers in certain areas (e.g., *T. cupira, testacea musarum, nigerrima*). In other cases the spaces between layers are largely filled in some parts of the nest or even over the whole nest, making a far firmer, heavier protective wall than the cerumen layers themselves provide. Our series of nests of *T. corvina,* which is the outstanding example of this development, seems to show that, as would be anticipated, young nests lack this material (fig. 119) while old nests are completely surrounded by it (fig. 114). Deposition begins first in the upper part of the nest of *T. corvina,* but species are not alike in this respect.

In *T. spinipes,* a close relative of *T. corvina,* deposition appears to start on one side of the nest and does not extend around the nest. As it grows larger, the earthen deposit forces the brood chamber toward one side of the nest (**Marianno,** 29). The deposit has been called a scutellum because it is often shield–shaped, although sometimes U–shaped, in *T. spinipes;* it has been discussed in detail by **Nogueira–Neto** (39). Only in this species, so far as known, is the deposit on one side only and shield-like. The name is therefore inappropriate for general purposes; for lack of a more suitable term we use the expression earthen material.

Many and perhaps all stingless bees have deposits of wastes in the nest, but they are usually rather limited in size. The enormous extent of the similar material of *T. corvina* and its relatives is probably the result of adding earth, plant fibers, excrement, propolis, etc. In the oldest nest of *T. corvina* studied, our impression (not verifiable) is that the material was encroaching on the storage and brood areas which were therefore reduced in size. Marianno, according to **Nogueira–Neto** (39), also noted that the larger (and older) the earthen deposits of *T. spinipes,* the smaller the size of the colony, a conclusion doubted, however, by **Nogueira–Neto** (39).

The earthen material has been observed only in exposed nests of the subgenus *Trigona (corvina, spinipes, amalthea, nigerrima, silvestriana)* and in the partially to largely exposed nests of *T. cupira* and *testacea musarum* in the subgenus *Partamona.* It may have some protective function for exposed nests—perhaps temperature or predator related, but young colonies must survive without it.

3. **Involucrum:** The involucrum is absent in nearly all forms that arrange brood cells in clusters (figs. 24–25a), presumably as an adaptation to nesting in restricted cavities, but is present (one layer, sometimes incomplete) in *T. australis* (fig. 4), an Australian cluster maker, and in the related *T. cincta* which also does not put cells in combs. The involucrum is also sometimes absent in some species that make combs of cells, as shown in column 16, Table 4, but this absence is not necessarily a specific character. In most cases where a nest of a comb–making meliponine is known to lack an involucrum, other nests of the same species have the involucrum. *T. remota* and certain species of the subgenus *Trigona,* some of them with irregular combs, appear to be exceptions, being comb–making species that regularly make no involucrum.

As shown in column 17, Table 4, many species have laminate involucra several layers thick. In the most typical cases according to the present nomenclature (but not necessarily the most primitive or even most common species), there is a sharp distinction between rather rigid, usually dark, batumen layer or layers around the whole nest including the pots and one or more softer, more flexible, usually paler layers of involucrum around the brood chamber only and forming the walls of that chamber. However, as indicated in column 19, Table 4, in various forms in which the batumen, involucrum, or usually both are laminate, such a distinction breaks down and the pots may be scattered among different layers, further confounding the distinction. This is especially true of some species of ***Trigona***

(Trigona).

4. **Functions of multiple enveloping sheets:** Laminate batumen and involucrum are common, as shown in columns 12 and 17 of Table 4. The special functions of protection against physical blows or attack by moderate–sized or large animals have been discussed above under batumen of exposed nests. A more general function commonly postulated is protection against temperature fluctuations. This seems probable, especially when layers are numerous, and the view is supported by the numerous enveloping sheets characteristic of exposed nests (except for those of some *Paratrigona* in partially shaded places). Moreover the total thickness is greatest on the upper part of the nest, for example in *T. corvina,* supporting the idea that the layers serve for insulation (figs. 114, 119).

But within the ground or in a tree trunk the case for the function of laminations in temperature control is less clear. Nests in thin–walled natural tree cavities or in boxes are no more prone to multiple layers than are nests in the soil or in thick trunks. The real function of lamination in cavities is probably to occupy space, i.e., to reduce the size of the cavity to that appropriate for the nest of the species concerned.

There are many pillars and connectives in some nests, for example those of *T. carbonaria* and *testaceicornis perilampoides,* which form anastomosing complexes that fill in excess space, much as enveloping sheets do in other species. Indeed, pillars and connectives may expand, become fan–shaped, and unite to become enveloping sheets in some parts of a nest. This sort of development is extreme when one transfers a nest of such a species into a box that is too large. The bees seem to try to fill the whole box, except for the nest portion, with pillars (**Michener,** 32; *T. t. perilampoides,* fig. 77).

It seems at least possible that multiple protective layers have the added function of providing space on which the large populations of adults can rest. Many species act as though they abhor large empty spaces in the nest. For example, it is common to find one or two temporary sheets of involucrum–like material in the space between the advancing front of new cells and the old cocoons from which bees are emerging (fig. 70). Such sheets must be constantly removed and reconstructed as new cells are built and old cocoons removed. The only function that we can imagine for them is providing resting space or surfaces for the movement of bees working on the new cells or removal of old cocoons. Yet such sheets are obviously not necessary, for if there is little space above the advancing front, they are absent.

An untouched source of possible characters is the manner in which enveloping layers, especially when there are several or many of them, are separated from one another and supported. There is little in the literature on the subject and our own observations are frequently lacking in detail at this point. In many cases the layers broadly attach to one another, so that one sheet often appears to split and to rejoin others. Carried to an extreme, this pattern produces the cellular aspect mentioned earlier in discussing batumen. Other species have pillars between and supporting the layers, but the pillars are sometimes flat and themselves sheet–like, thus merging into the pattern of interconnecting sheets. The sizes and locations of the openings that allow the bees access to the spaces between layers should also be studied. When such matters have been recorded it may be easier to understand the functions of protective layers.

F.— Storage Pots

Pots for the storage of honey and pollen are made of soft brown cerumen which occasionally becomes hard and dark with age. They are usually thin–walled but a few species add cerumen to the outside so that the lines between pots become obscure. They are typically located inside the batumen and outside of the involucrum. They are sometimes isolated, usually in groups, and sometimes all in one enormous mass. No species is known in which the pots are consistently isolated, although they are rather well separated in *T. sp. B.* The pots or groups of them may be directly attached to the lining batumen or to other nest structures but often the pots are supported on short pillars or connectives and thus not directly attached to any of the enveloping sheets. Column 23, Table 4, shows the positions of pots with respect to the brood chamber. This feature is often plastic in unusual nest sites like an artificial hive or even a horizontal hollow tree but seems characteristic in undisturbed natural sites.

Approximate shapes and sizes of pots are shown in columns 20 and 21, Tables 4 and 5. Isolated pots are round in horizontal section, but pressure from neighbors results in flat common walls and prismatic shapes for pots that are pressed together in groups. **Moure, Nogueira–Neto** and **Kerr** (36) have indicated that pots of *Meliponula bocandei* are different from those of other Meliponini because of being hexagonal in shape but to us this seems to be merely the result of pressure from neighbors. There is nothing in accounts of nests of this species to show that its pots differ importantly from clustered pots of many other species. We have not seen nests of *M. bocandei*, however.

Pots are not of uniform size or form. There are variations within a single nest, the smallest pots sometimes being less than half as long or wide as the largest ones. Nonetheless, in a general way pot size is characteristic of the species, as Table 5 shows. Also, in general, pot size is positively correlated with worker size, but there are many exceptions, as shown by the rather small pots of the subgenus *Trigona* which contains rather large bees and the relatively large pots of the small *T. quadripunctata quadripunctata*.

Pots of *Lestrimelitta* all contain like material, a mixture of pollen and honey. This is because these robber bees, which do not visit flowers, carry pollen from the host nests mixed in the crop with honey instead of externally on corbiculae. Possibly the presence of much pollen is responsible for numerous reports (63) that honey of *Lestrimelitta* is poisonous.

In all other stingless bees some pots contain pollen, others honey. Only rarely does one find a pot containing both materials, and even then they are not mixed but are more or less separated.

Honey pots and pollen pots sometimes seem miscellaneously mixed but usually there are groups with each material, although the groups may be partially mixed. Sometimes the pots in one part of the nest contain pollen, in another part, honey, and in *T. buchwaldi*, pollen and honey pots are separated by a wall of cerumen (fig. 81; column 22, Table 4).

Ordinarily honey and pollen pots have the same size and form, sometimes modified by the fact that the liquid contents of the former allow more slumping with age than the firm contents of the latter. In most species the pots are roughly spherical or oval (figs. 39–41). As shown in columns 21 and 22, Table 4, however they are strikingly elongate in the species of *Trigonisca* (fig. 32) and in a few species of *Tetragona.* In one of these, *T. flavicornis,* pollen pots are broad above and tapering below while honey pots are spindle–shaped; both are elongate. In a few other species of *Tetragona,* the pollen pots are elongate while honey pots are short oval. These are the only meliponine bees in which honey and pollen are stored in markedly different containers.

G.– **Brood and brood chamber**

1. **Brood areas:** The most striking characters found in meliponine nests have to do with rearing of the brood. In species inhabiting planiform nests and slender tubular cavities, brood cells are made in clusters here or there in the nests (**Michener,** 32; **Pooley** and **Michener,** 43). There is no specific brood rearing area. Clusters of brood cells or cocoons may be rather distant (fig. 102). Hence there is no brood chamber. Such forms are *Hypotrigona, Trigonisca,* and some species of *Plebeia* and *Tetragona,* especially *T. fuscobalteata* subsp. and *clypearis,* and probably *Lestrimelitta cubiceps.* These species are small to minute, perhaps another factor other than the lack of combs of cells that permits the use by these species of flat, tubular, or irregular small nest cavities. One of the largest members of the group is *T. (Tetragona) nigra paupera.*

Other meliponines have brood chambers, normally only one per nest although occasionally more. These are relatively regular areas of substantial diameter, usually surrounded by an involucrum. Shapes and sizes of brood chambers vary as indicated in columns 24 and 24a and b, Tables 4 and 5. Shape varies in part according to the shape of the nest cavity and should not be stressed in evaluating relationships until more is known.

The brood chamber of *T. iridipennis* may be quite small and irregular, grading toward the planiform or irregular cavities utilized by *T. clypearis* and *fuscobalteata* subsp. However, so far as known, there is only one cell cluster and hence a brood chamber can be recognized. In *T. cincta* and *australis* the cell clusters are also single and large; moreover the presence of an involucrum defines the brood chamber (fig. 4). Other forms have groups of combs or at least of cells showing considerable layering and suggesting combs (as in *T. hockingsi).* This arrangement is only possible in the somewhat spacious area provided by a brood chamber.

Multiple brood chambers in a single nest are recorded for *T. chanchamayoensis, T. lurida, T. cilipes,* and *T. frontalis* (fig. 16). In all cases there was only one nest entrance and one queen, so far as known. Therefore each nest must represent the work of a single colony and the queen must move from chamber to chamber. So far only one nest with multiple chambers has been found in each species listed above, but in some cases this is the only known nest for the species. It is possible that multiple chambers are common in nests of some species.

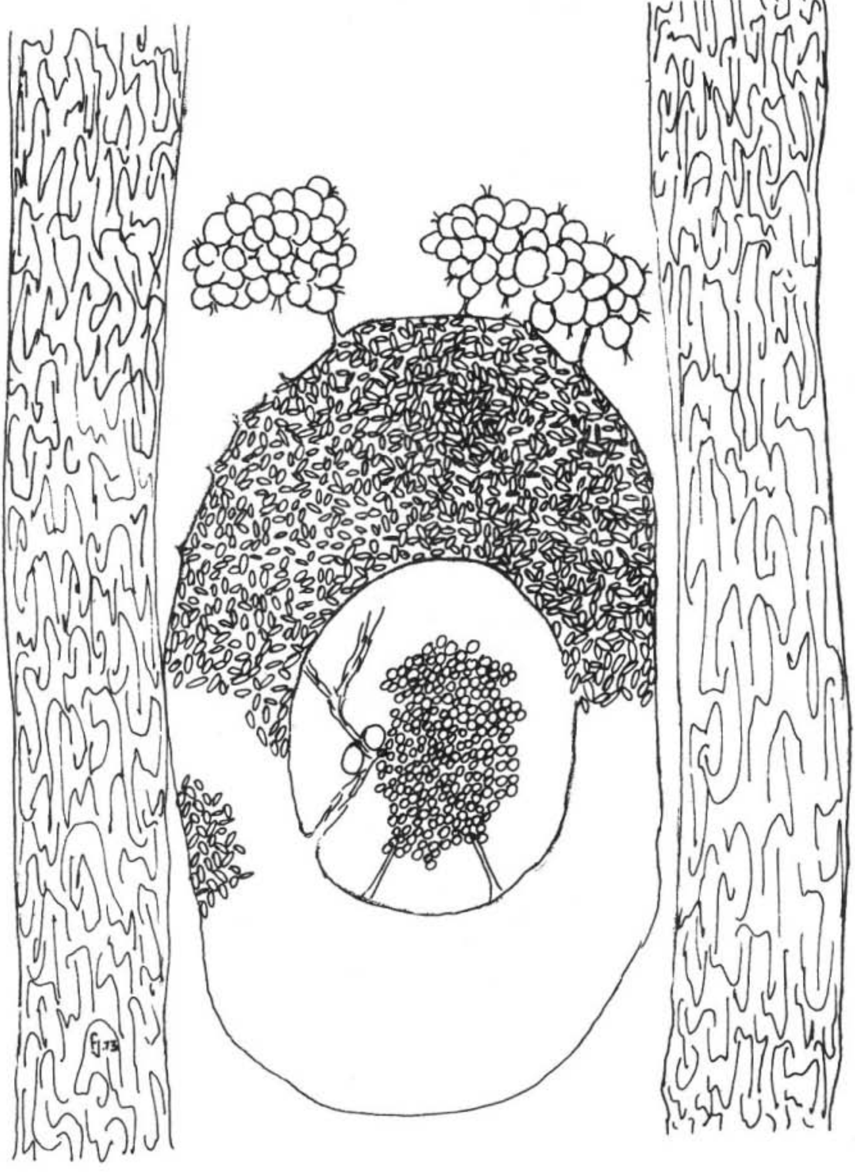


Figure 4. Diagram of part of nest of *Trigona (Plebeia) australis*, (*sp.* 7), a cluster maker that also makes an involucrum (from *Michener*, 32).

2. **Brood cells and cocoons:** The shape of the brood cells is shown in column 25, Table 4. In two species, *T. australis* and *cincta*, the cells are spherical (figs. 5, and 6). In a few others, classified as subspherical, the cells are short oval, varying occasionally to spherical, and in a number of other species the cells are oval. In these forms the cells are not crowded but are in clusters or relatively loose layers or combs. In the remaining species, the cells are crowded together into horizontal combs and each cell is therefore elongate, parallel–sided with rounded ends (fig. 67)

Spherical or near spherical cells become oval when the prepupal stage is reached and cocoons spun. At this time the larva or prepupa in each cell straightens out, with the result that the cell is strectched slightly and is no longer spherical (fig. 6).

The construction and provisioning as well as egg deposition and closure of cells are relatively well known in Meliponini and require only brief review here. Each cell is constructed of pale soft cerumen with a high lip around the opening (figs. 128, 137). It is then provisioned and an egg laid in it by the queen. Peculiar features of the egg laying ritual have been described in detail by Sakagami and coworkers (references in **Sakagami** and **Zucchi**, 51, 52, 53). A worker then closes the cell, drawing the material of the lip inward to form a closure.

Dr. S. F. Sakagami pointed out to us, on a visit to Costa Rica, that some species construct cells continuously and asychronously so that an advancing front has cells in various stages of construction, while other species construct cells synchronously (fig. 139 appears to show synchrony), so that at any one time all the new cells in an advancing front will be at the same stage. We have since then recorded this character when possible, and the results are incorporated into column 25, Table 4. A question mark after an S indicates that no new cells were being made but this circumstance suggests synchrony.

In several species cerumen is added to the outsides of the cells a day or two after they are made, making the division lines among cells inconspicuous. Thicker walls in older cells than in new ones demonstrate this behavior in *T. sp. A* and *iridipennis*. Occasionally the cells become embedded in a seemingly solid layer of cerumen, so abundant is the added material, both in some cluster makers like *T. iridipennis* and some comb makers like *T. corvina*. On the other hand in the cluster maker *T. nigra paupera*, there is at no stage much cerumen between the cells.

After the larvae are fully fed and have constructed their cocoons, much of the cerumen is removed. In cluster makers only enough is left to support the cocoons (fig. 103); usually this means short connectives or pillars between adjacent cocoons. In comb makers, cerumen between cells cannot be removed because the bees cannot get at it, the cocoons are therefore held together in combs (fig. 18). But cerumen from the ends of the cocoons and from the margins of the combs is removed. After emergence of adult bees the cocoons are removed. There is thus no reuse of cells but only of the materials of which they are built.

Removal of wax usually occurs first from the tops of cocoons and later from the bottoms. Removal of cocoons is usually on an individual basis; as soon as a bee has emerged, its cocoon is destroyed. However, occasionally only the upper parts of cocoons are removed so that a comb of cocoon bases remains. Four such combs were found in each of two nests of *T. frontalis* (figs. 15, 16) and one in a

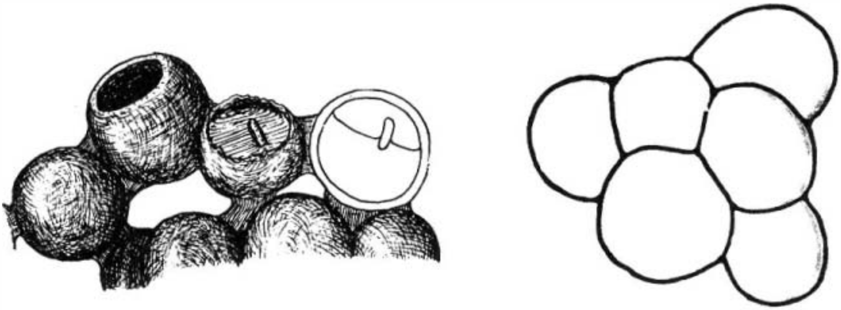


Figure 5. Cells of *T. (P.) australis* (*sp.* 7) (from *Michener*, 32).

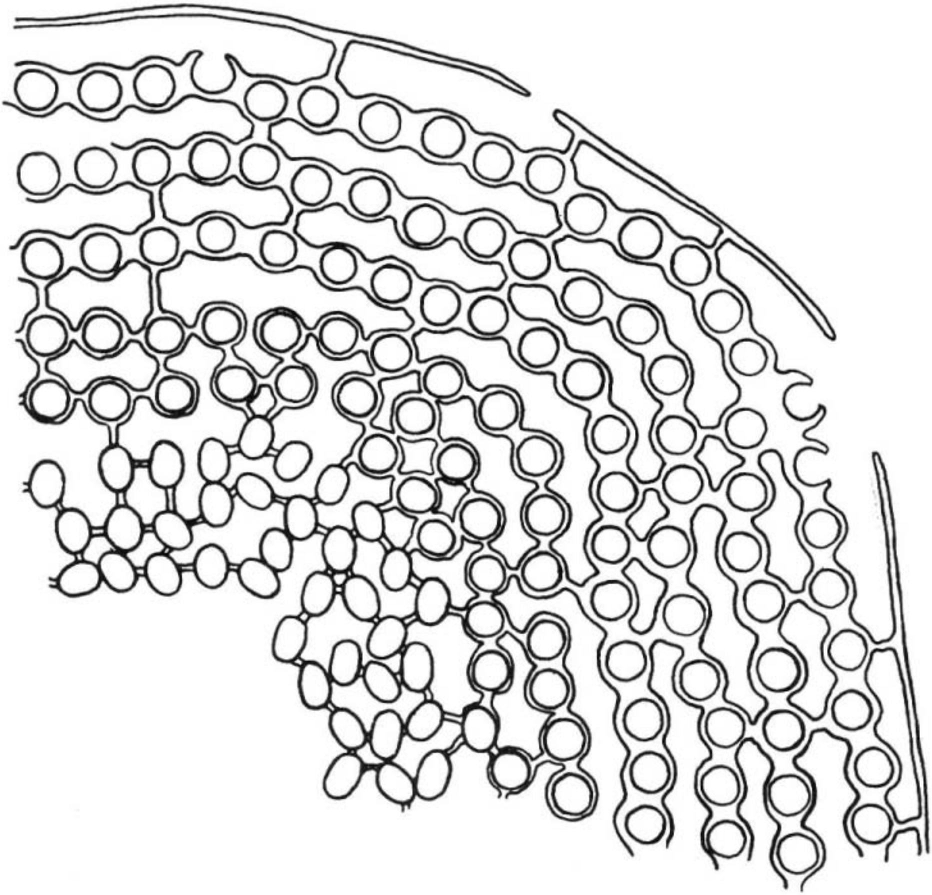


Figure 6. Cell layers of *T. (P.) cincta* (*sp.* 8) (from *Michener*, 32).

nest of *T. sp. A*. Rarely thin laminae of cerumen (called trochoblasts by **Ihering,** 18, 21) bearing the pattern of cocoon bases may survive as involucral sheets if in the proper position, as discussed in the section on dynamics of the brood area. They indicate failure, probably in colonies of decreasing populations, to remove cerumen from the lower surface of a comb of cocoons. In one nest of *T. corvina* some cocoon layers were still fully covered with cerumen and looked like combs of cells, or only tops of cocoons were exposed; on emergence of the bees an early stage in production of a patterned layer was noted (fig. 118). No such patterned layers exist in actively used parts of a brood chamber. Such layers have been noted in nests of such unrelated bees as *T. corvina, jaty jaty, cupira, postica, molesta,* and *L. limao* (50, 63).

As is well known, queen cells of *Melipona* are the same size as worker cells, intermixed with them, and extraordinarily numerous considering that most of the young queens are killed by workers. In other genera queen cells are large and relatively few in number. While sometimes intermixed, they are usually marginal, i.e., at the margins of combs or in the outer parts of cell clusters. The character of queen cell size is so well known and correlated with the recognized generic classification that it is omitted from Table 4 although it appears in Table 5.

There may be none or only one or two queen cells in a *Trigona* nest. Very large numbers are 15 in a nest of *T. silvestriana*; 19, *T. corvina;* 22, *T. dorsata*; and 26, *T. fuscipennis.*

3. **Brood cell arrangement:** The arrangement of brood cells is related to the size and regularity of the space occupied by the nest. Species that make cells in clusters often occupy thin spaces (planiform nests), slender tubular spaces, or highly irregular spaces in which an organized cell arrangement would not fit. The lack of an involucrum is also a necessity for occupancy of such spaces. The cluster makers that have an involucrum, *T. australis* and *cincta,* occupy spaces that could be utilized by intermediate types or by comb makers.

Cluster makers like *T. nigra paupera* and *silvestrii* that make well separated cells, and probably all cluster makers, construct cells with independent walls, i.e., each cell is separated by a space or at least by a double wall from its neighbors. The same seems to be more or less true of forms having oval cells even when these are to varying degrees organized into combs as in *Dactylurina.* But in those having fully developed horizontal combs, a new cell is constructed at the edge of the comb using the existing cell walls as part of the wall of the new cell. Crowding leads to parallel walls, and more important, between adjacent cells there is only one cell wall instead of two as in cluster makers and others like *Dactylurina.* One of the advantages of comb construction must be the economy in the use of cerumen that results from this arrangement. On the other hand, the cluster arrangement, while costing more in cerumen for cells, opens up to a species a variety of cavities that would otherwise not be suitable.

As shown in column 26, Table 4, numerous species in systematically scattered positions make unstructured clusters of cells (figs. 5, 28, 103). In most of them the clusters may be in various parts of the nest, there being no brood chamber, but as indicated above, the cells are all in one cluster in *T. iridipennis* and *australis* and even have an involucrum around them in the latter. In *T. silvestrii* (one nest), the cells were all in one area but perhaps this is not always the case.

Relatively few species show intermediates between unstructured clusters of cells and the usual organized combs. However, such intermediates are of special interest. Two unrelated species, *T. cincta* (fig. 6) and *araujoi*, have the cells as in a cluster but organized into somewhat irregular concentric layers. Other, also unrelated, species (marked IC in Table 4, column 26) have cells organized into small patches of somewhat irregular comb, sometimes with some cells between such patches and not forming part of any comblike area. A few species (BC in the table) have cells organized nicely into regular comb, but the comb broken up into patches (figs. 125, 130). This may not always be a specific character. Thus the nest of *T. fulviventris* described below had such combs, while previous descriptions indicate ordinary combs. Similarly irregular comb showing signs of spiraling is marked IS in the table.

The majority of Meliponini have the brood cells opening upward and crowded together to form more or less horizontal comb. Usually the combs are independent, horizontal or rarely slanting (*T. ornaticeps*, fig. 62; *T. molesta*, Schwarz, 63). In other species the comb is a single broad spiral (fig. 80). The spiral arrangement is much less common than independent combs but occurs in various unrelated groups. The difference between the two may not be very fundamental since there are records of brood chambers containing some independent combs followed by several layers made up of a spiral (**Schwarz**, 63). The number of combs indicated in column 27, Table 4, is either the number of independent combs or number of turns of the spiral, depending on the species.

Finally, a single species, *Dactylurina staudingeri*, has vertical double combs, each consisting of two layers of horizontal cells opening in opposite directions, as in *Apis*.

The directions of the principal axes of cells and cocoons are important in understanding them, as in most other groups of bees. In the Australasian species of *Plebeia*, *T. australis* and *T. cincta*, as well as in at least some species of *Trigonisca* (*T. buyssoni*), the cells open upward or laterally at various angles (Figs. 5, 112) and axes of cocoons are similarly erratic. In some of these species there may even be some cells opening downward.

In *T. silvestrii*, while axes of most of the cells are vertical, some are reputedly not. In making this statement **Ihering** (20) could have been referring to cocoons that had come loose and later been fixed in oblique or horizontal positions, for they are connected only by short, slender pillars.

In other cluster makers as well as those that make irregular as well as regular combs (except for *D. staudingeri*), cells open upward and cocoon axes are vertical. There are exceptions to this statement, as when combs are sloping or curved. A more accurate statement is that the principal axis of a cell or cocoon is at right angles to the plane of the comb at that point. This last statement even applies to *D. staudingeri*.

4. **Dynamics of the brood area**: A nest has a limited volume and it is clearly impossible for bees to build an advancing front of new cells progressing forever upward. They would soon reach the limit of the nest. They therefore reuse the brood area over and over. In *T. australis* and *cincta* new cells are added to the outside of the cluster, which is therefore the advancing front, until emergence of

the bees from the oldest area, i.e., in the center of the cluster, leaves a space. New cells are then begun again there. The advancing front therefore moves repeatedly upward and outward, perhaps also downward, as shown by **Michener** (32) (fig. 7).

In at least two species with separate combs, *T. denoiti* and *lendliana* (**Smith,** 68; **Portugal–Araújo,** 46), the advancing edge of each comb develops rotationally and there is no advancing front. Cocoons are vacated along an irregular radius of the comb, and new cells are constructed along another irregular radius, an advancing edge, that follows the first, there being a gap between the two radii. Thus instead of forming new combs or new turns of a spiral, the old combs are constantly being reconstituted (fig. 11). This method is similar to that of spiral formation except that the advancing edge follows directly behind the retreating edge of old cocoons. To make a spiral the advancing edge must rise above and overlap the retreating margin.

For all other forms except *D. staudingeri,* advancing fronts move only upward. In most cluster makers there may be several clusters in different parts of the nest, each with an advancing front. Sometimes it seems that new clusters in new places are started as necessary. Other clusters in the same nest may show new cells at or near the bottom, separated by a space from the retreating zone of cocoon emergence and removal, indicating reuse of the same space for brood. This is the rule in *T. iridipennis* whose clusters are single and compact (fig. 8). The only nest studied of *T. hockingsi*, a form that makes very irregular combs, had four advancing fronts in a single brood chamber in a tree cavity. This suggests that this species, like many cluster makers, may be able to use more slender or irregular cavities and have several separated brood areas.

In forms with cells in layers, an advancing front involves those layers that still have advancing edges (fig. 9). New layers start at or near the center either by erection of a new central cell or by spiraling. When combs are separate, each new one is started by a median cell constructed alone on top of a short pillar above the center of the preceding comb (fig. 14) or if there are permanent pillars, on one of them (fig. 45). New cells are then added laterally, around the median cell. The advancing edge is therefore circular (fig. 12). As the comb expands, pillars from the comb below are supplied to support it. When the new layers are produced by spiraling, there is no starting of independent new combs. The advancing edge climbs continually above the preceding layer at the center, and then expands laterally. The advancing edge itself is therefore also a spiral (fig. 13). New layers, whether produced as separate combs or by spiraling, are nearly always started before the preceding two or three reach maximum diameters. The conical pattern produced by the advancing edges is the advancing front (fig. 9).

Comb making forms usually have only one advancing front per brood chamber. There is a partial exception when the front reaches the top of the chamber and a space develops at the bottom due to removal of empty cocoons. New combs are then started at the bottom while new cells are still being added to the advancing edges of one or two combs at the top. The movements of the front upward, and of the advancing edges outward, are shown diagrammatically in fig. 9. The situation is not basically different in forms with spiral combs than in those with separate combs except in the manner in which the layers of cells originate. Two or three advancing fronts at different levels occur in *T. spinipes* (**Ihering,** 18,

21) and *corvina*.

In several unrelated comb-making species (*T. jaty, capitata capitata, lendliana, mirandula*) nests are sometimes found in which the combs are divided vertically by a small space, on a plane more or less through the center of the cluster. Thus the brood chamber contains two (or in one case three) slightly separated parts on different time schedules (figs. 91, 92). That is, the advancing fronts are at different levels in the two (or three) parts. How such a situation arises is unknown but its maintenance is easily understood if the advancing fronts move at the same rates.

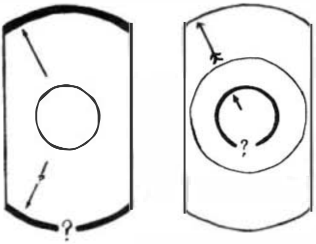
It has been suggested (**Schwarz,** 63) that a single advancing front might move continually upward without returning to the bottom of the chamber and that this could be possible if, as cocoons are removed, the layers of cells above slump down into the space made by cocoon removal. This is clearly not the ordinary situation. If it were, one would always find the advancing front at the top of the brood chamber. Yet slumping of combs does occur. We have seen trochoblast sheets in a nest of *T. corvina* whose brood area apparently had diminished. Sheets showing the cocoon pattern could be seen forming parts of the enveloping sheets for about 1 cm lateral to the edges of the combs. This indicated that the brood chamber had formerly had a larger diameter. And at the bottom of the brood chamber were 4 or 5 nearly intact sheets of the same material. These sheets were only about 1 mm apart. Their presence indicates not only a shortening of the brood chamber but also slumping of combs, for the sheets were much closer together than bases of occupied comb layers, which in this species are separated by about 10 mm. In *T. frontalis* and *sp. A* a comparable behavior is removal of only top halves of cocoons, so that a layer of cocoon bases results (figs. 15, 16, 20, 21); these sometimes are closer together than if no slumping occurred.

The unique vertical combs of *T. staudingeri* are also unique in the developmental sequence, for the advancing fronts of all combs move downward together (fig. 10). When bees emerge from cocoons at the tops of the combs, the space is filled with branching supporting pillars. New cells are soon begun at the top, and the advancing front moves down, a gap with pillars preceding it. There is an incomplete or largely complete horizontal sheet usually constructed in or just below this gap, just as in many other forms a sheet often occupies space above an advancing front. The new combs are not necessarily the same in number or orientation as the old ones being destroyed by emergence of bees.

5. **Pillars:** The use of pillars and connectives in peripheral parts of nests, seemingly to fill in empty space, has been discussed above. In the brood chamber, however, pillars are of considerable functional and systematic importance. As a layer of cells expands, short pillars are constructed at intervals of several cell diameters to support the new comb. These short temporary pillars between combs are sometimes removed or greatly reduced in numbers when the cerumen is removed from the cocoons. In other species they are not removed until after emergence of the adults, when the cocoons are removed and the comb destroyed. This character has not been recorded for many species but, when known, is recorded in column 28, Table 4. A small circle following an S means that the number of intercomb pillars is much less between combs of cocoons than between

Figures 7–13. Diagrams of dynamics in brood chambers. Black = advancing fronts and edges, i.e., where new cells are being added. Arrows show developmental sequence of brood from the heads, indicating eggs, to the tails, indicating emergence of adults. 7. Vertical sections through brood chamber of *Trigona (Plebeia) australis.* (*sp.* 7). 8. Same for *T. (Tetragona) iridipennis.* (*sp.* 83). 9. Same for comb of spiral making species. 10. Same for *Dactylurina staudingeri.* (*sp.* 116). 11. Top view of a comb of *T. (Meliplebeia) lendliana* (*sp.* 3). 12. Top view of advancing front of comb making species. 13. Same, for spiral making species.

Figure 14. New cell, starting new comb.



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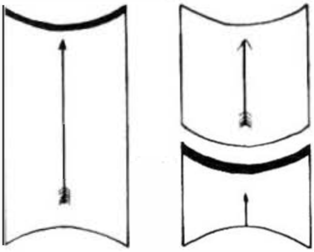

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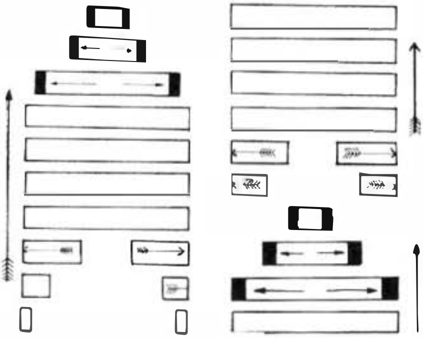

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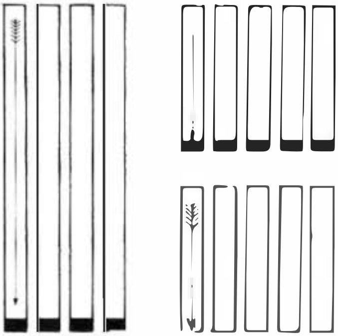

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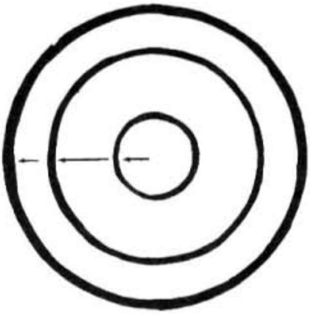

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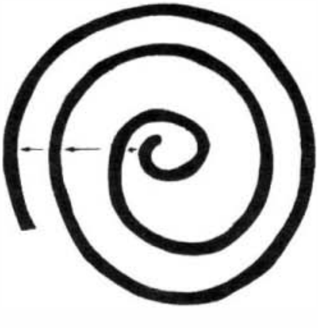

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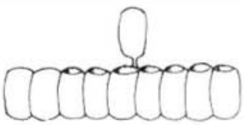

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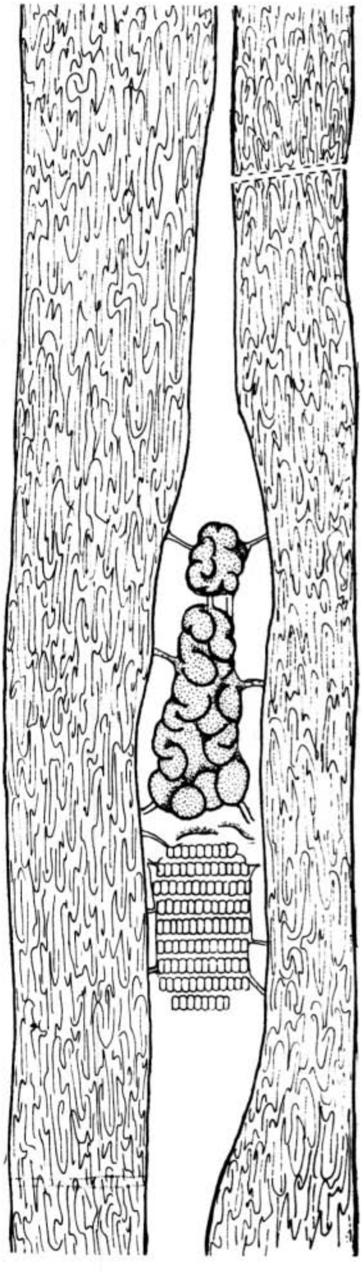
Figures 15, 16. *Trigona (Plebeia) frontalis*, (*sp.* 12), diagram of nest.



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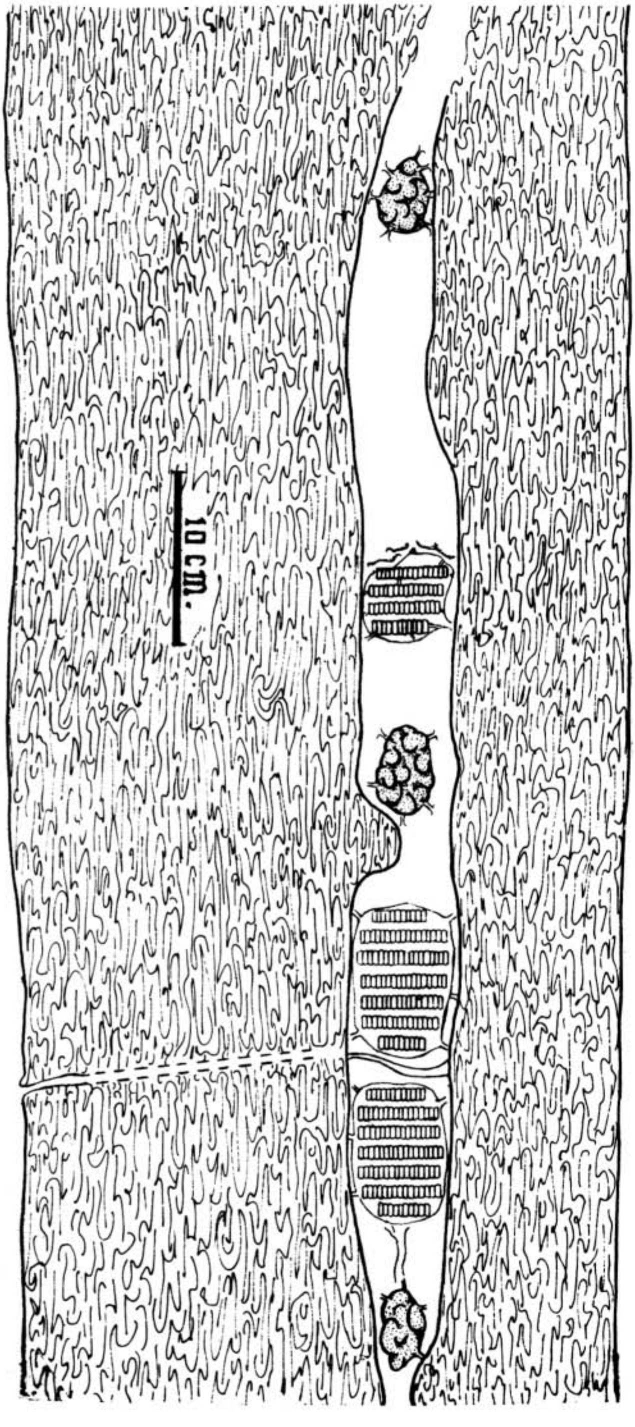

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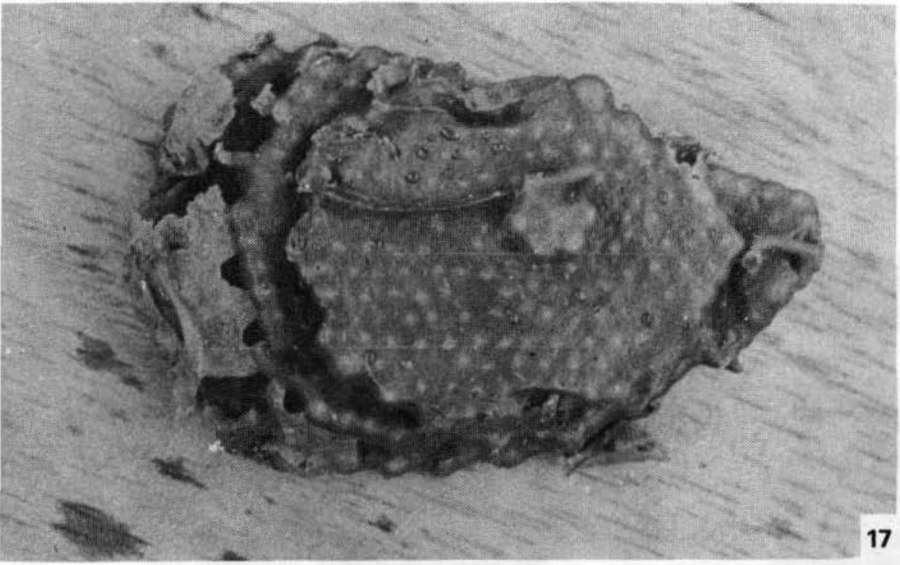
Figure 17. *T. (P.) frontalis,* (*sp.* 12), top of comb showing fusion of cells by cerumen, and bits of involucrum marginally.

Figure 18. *T. (P.) frontalis,* (*sp.* 12), comb of cocoons showing queen cocoon not at margin and bits of involucrum marginally.



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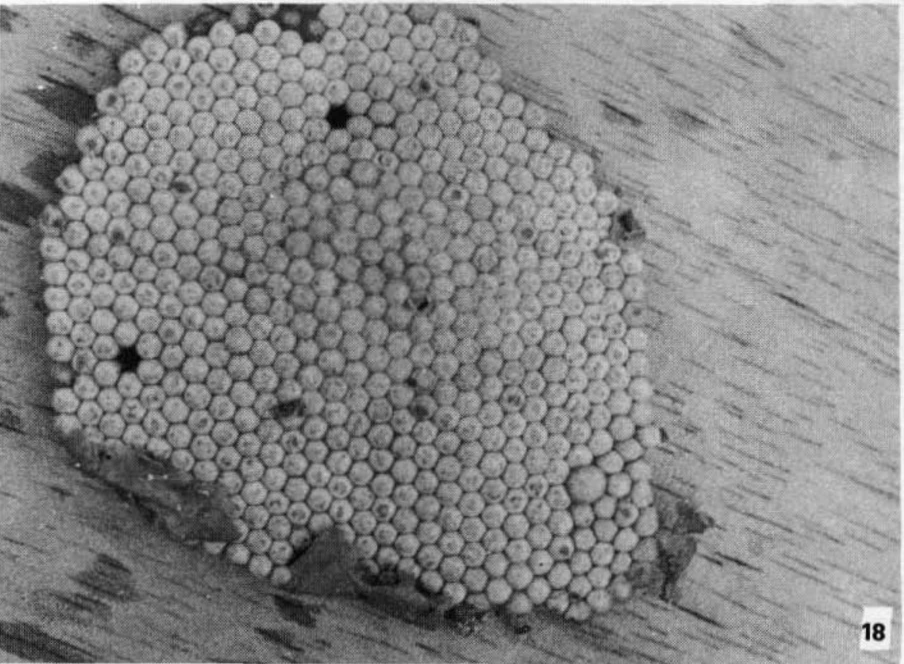

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Figure 19. *T. (P.) frontalis* (*sp.* 12), brood chamber showing very incomplete involucrum of nest 1.

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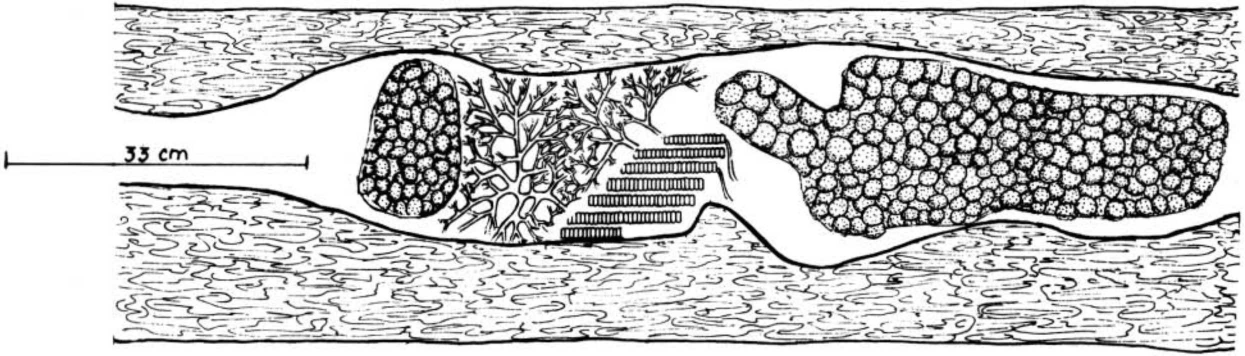
Figures 20, 21. *Trigona (Plebeia)* sp. A (*sp.* 18), diagram of nests.

Figure 22. *T. (P.)* sp. A (*sp.* 18), nest entrance.



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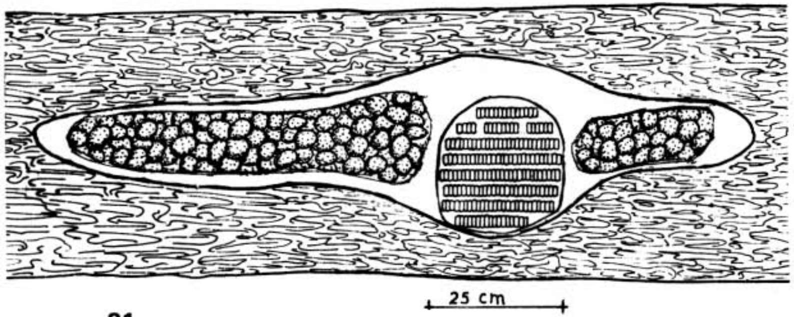

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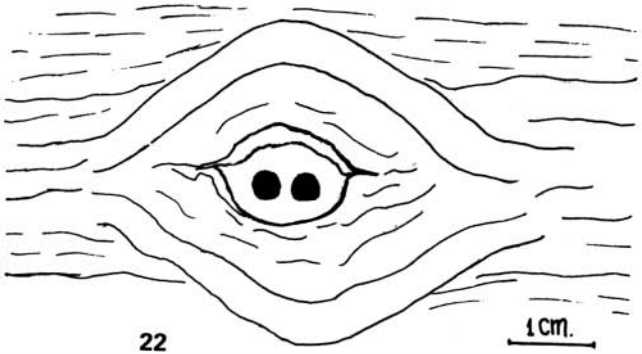

22

combs of cells; a + means that the number of such pillars is about the same. When the combs are left supported only or mostly at the margins, they may sag. This may account for the concavity of combs of some species.

As shown in column 28, Table 4, however, there are two groups, *Partamona* and certain species of the subgenus *Trigona,* in which there are strong and presumably permanent pillars passing through the brood chamber and out for some distance into the surrounding layers. These pillars are slender and have long straight sections in *Partamona* (figs. 39–42, 44, 47 but are coarse and irregular in the species of the subgenus *Trigona* (figs. 123, 124, 129, 133). They support the combs. At least in *T. fulviventris* and *cupira* and probably in others, the cell starting a new comb may be attached to the side of one of the permanent pillars (fig. 45) and in *T. fuscipennis* spiraling of combs is sometimes around pillars. This may account for some of the irregularity of the combs that we have seen of these species.

H.— **Costa Rican nests.**

Data on the various Costa Rican nests studied have been in considerable part presented above. The nest locations and sizes, or sizes of occupied parts of cavities, are given in Table 3. The basic characteristics of the nests are given in Table 4, and pertinent measurements in Table 5. However, certain details, together with photographs and diagrams to help to indicate the real appearance of the nests, are provided here. The species are numbered to correspond to species in the tables.

12. *Trigona (Plebeia) frontalis* (figs. 15 – 19). Nest 1; north of Quepos (fig. 15). Batumen plates absent; apparently not needed in a cavity of this size. Involucrum very incomplete, limited to irregular patches on sides of brood chamber, attached to edges of combs. Pots all above brood chamber, dark brown, compact and fused so that they are difficult to recognize individually from the outside, in two clusters, upper one of honey pots, lower of pollen. Clusters of pots supported by long pillars far from wall of cavity. Combs 14, plus four at bottom consisting only of bases of cocoons; upper two combs forming advancing front; pillars between combs absent between combs of cocoons except for a few between uppermost (youngest) cocoons.

Nest 2; Pozo Azul (fig. 16). Three brood chambers in a long hollow. One batumen plate present, between two of the brood chambers! Involucrum complete around each brood chamber, two layers thick below lowest chamber. Pots similar to those of nest 1, upper cluster containing pollen, others honey. Combs 8, 12, and 5 in the three chambers, plus four at bottom of upper chamber consisting only of bases of cocoons. Otherwise as in nest 1, advancing front at top of each chamber.

18. *Trigona (Plebeia) sp. A* (figs. 20 – 22). Nest 1 (in a tree trunk that had been cut a year before; fig. 20). Entrance consists of two small holes side by side, each about 3 mm in diameter (fig. 22), entering a larger tube extending through wood to brood chamber, in this tube, 2 cm from surface, is a framework of black pillars and plates. Batumen plates absent. Involucrum absent. Pots dark brown, on both sides of brood chamber, probably a reflection of horizontal position of log; honey and pollen pots mixed although there are areas of pollen pots and others of

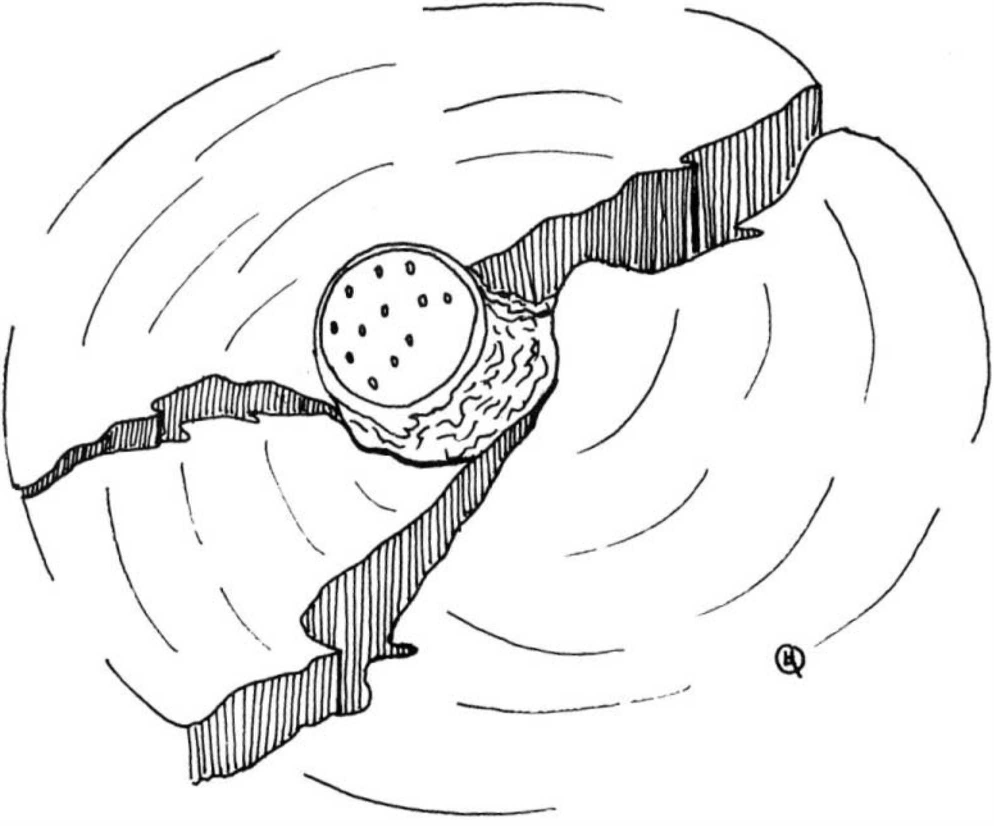

Figure 23. *T. (Plebeia) tica (sp. 21)*, nest entrance.

Figures 24, 24a. *T. (P.) tica* (*sp.* 21), nest.

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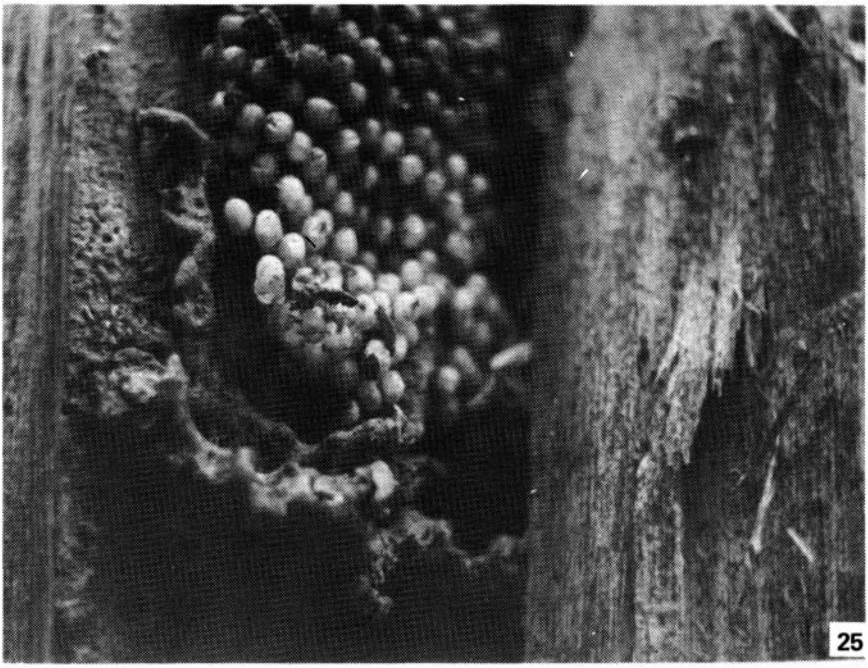
24a.

Figures 25, 25a. *T. (P.) tica* (*sp.* 21), part of brood.



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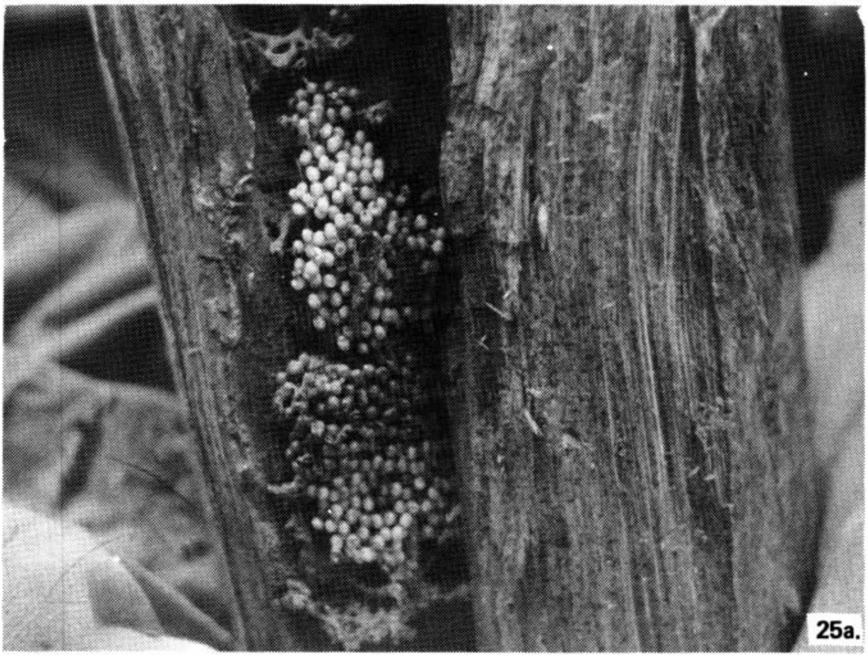

25a.

Figure 26. *Trigona (Nogueirapis) mirandula* (sp. 22), diagram of nest.

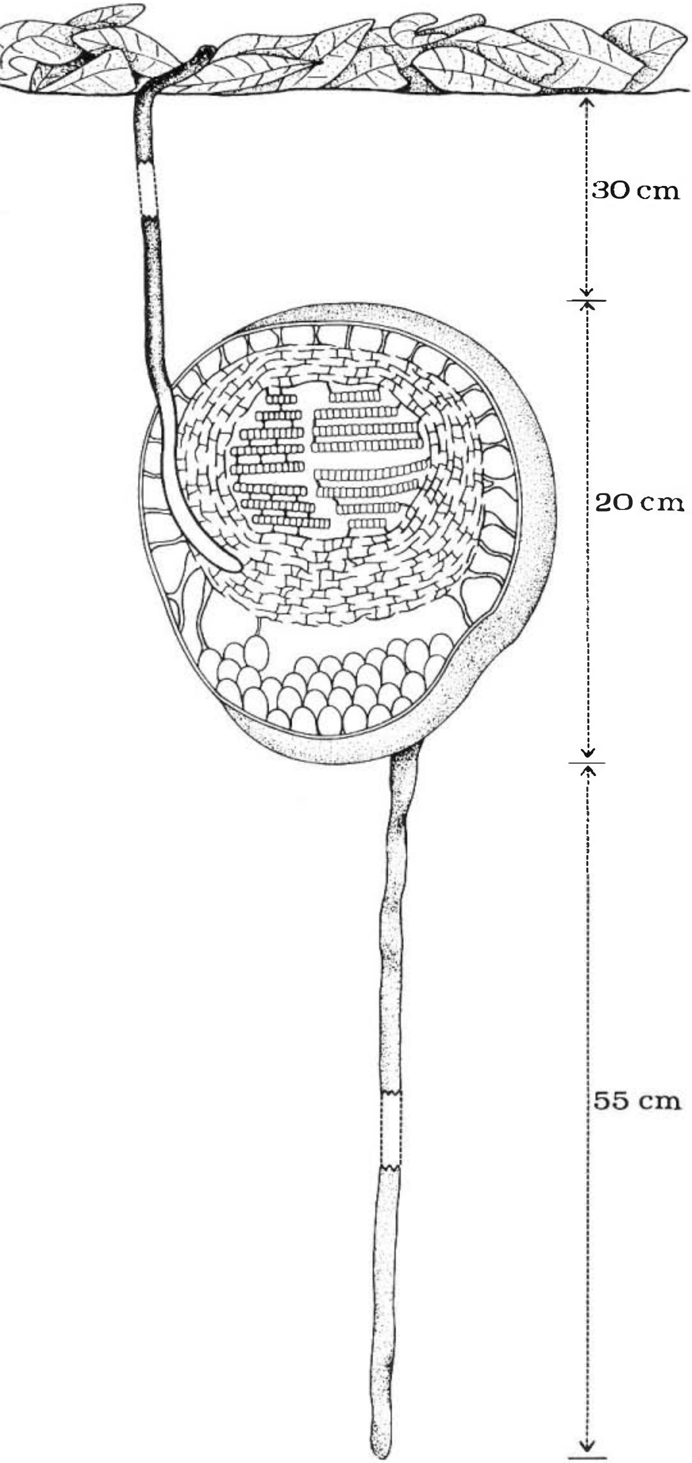
30 cm
20 cm
55 cm

Figure 27. *Trigona (Trigonisca) buyssoni* (*sp.* 30), nest entrance.

Figure 28. *Trigona (Trigonisca) buyssoni* (*sp.* 30), cells.

Figure 29. *T. (T.) buyssoni* (*sp.* 30), cocoons.


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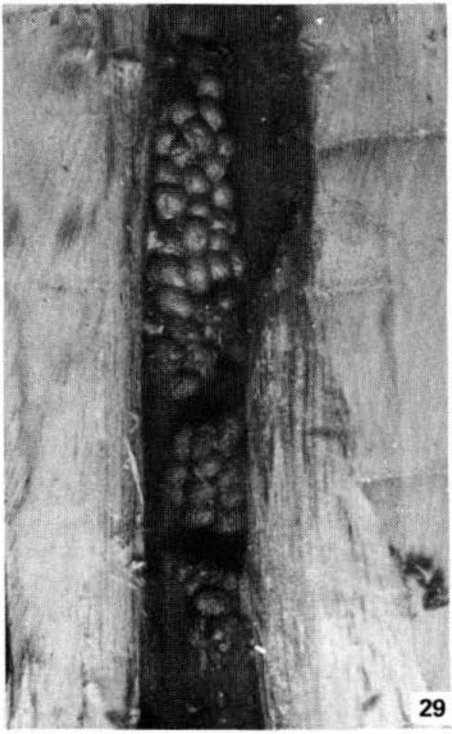
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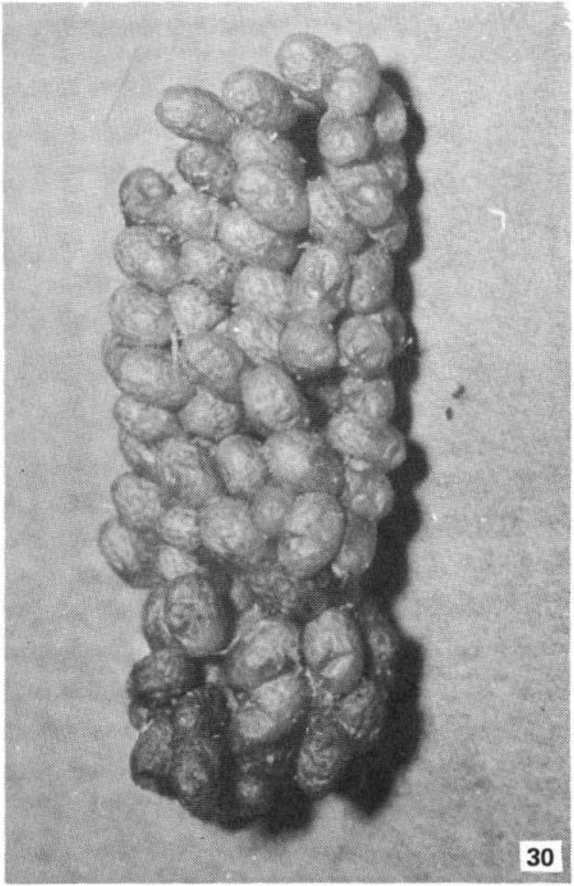
Figure 30. *T. (T.) buyssoni* (*sp.* 30), cocoons enlarged.

Figure 31. *T. (T.) buyssoni* (*sp.* 30), food pot.



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honey; pots crowded and fused but more or less recognizable from the outside nevertheless; clusters of pots and also combs supported in cavity by long pillars. Combs 10, only upper one with new cells.

Nest 2; (also in horizontal log; fig. 21). Entrance double as in Nest 1, also with black pillars and sheets inside. One to two layers of soft, pale involucrum around cells. Pots as in Nest 1 but honey and pollen pots not mixed, cluster of pots on one side of brood chamber all honey, on other side pollen near chamber, honey at a distance; pots so fully fused that individual containers are not recognizable from outside of cluster. Clusters of pots and involucrum supported by rather long pillars. Combs 12 plus one at bottom consisting of cell bases, supported by pillars and marginal attachment to involucrum. Advancing front of two combs, in cavity at base of brood chamber, no new cells at top.

Noteworthy features are the paired entrances in the only two known nests and the presence of an involucrum in only one of these nests.

Cell construction seems to be synchronized for in one nest no open cups were present while in the other there were nine, all in the same stage.

21. *Trigona (Plebeia) tica* (figs. 23–25a). Described and illustrated by **Wille** (75). Noteworthy features are the cluster arrangement of the cells, with clusters scattered up and down the nest although mostly below the food pots, an advancing front of new cells moving up through the principal cluster, the individually distinct although fused food pots, and the long internal entrance tube. All these features distinguish this species from the two species of *Plebeia* listed above.

The clusters are rather loose, with spaces in which bees can crawl among the cells, and larger spaces between cocoons which are united only by short, slender pillars.

22. *Trigona* (*Nogueirapis*) *mirandula* (fig. 26). Nest described and illustrated by **Wille** (72, 74). Distinctive features of the subterranean nests are the single thick layer of lining batumen supporting by long pillars the much laminated involucrum. Although the combs are coded Co in column 26, Table 4, they are actually somewhat irregular, some of them sloping at angles of up to 20°, and some joining in a spiral fashion.

29. *Trigona* (*Trigonisca*) *atomaria*. The single partial nest examined contained only small irregular clusters of cocoons scattered along the nest cavity.

The workers were dichromatic, 55 yellow and 20 black.

30. *Trigona (Trigonisca) buyssoni* (figs. 27–31). The following notes concern the nest recorded in Table 3 in a cerambycid burrow. Internal entrance tube of gray material, about 3 mm in diameter and 15 mm long, directs traffic along the nest cavity from the entrance. Pots only five, all isolated (fig. 31), made of thin, light brown, soft cerumen, and supported by several short pillars.

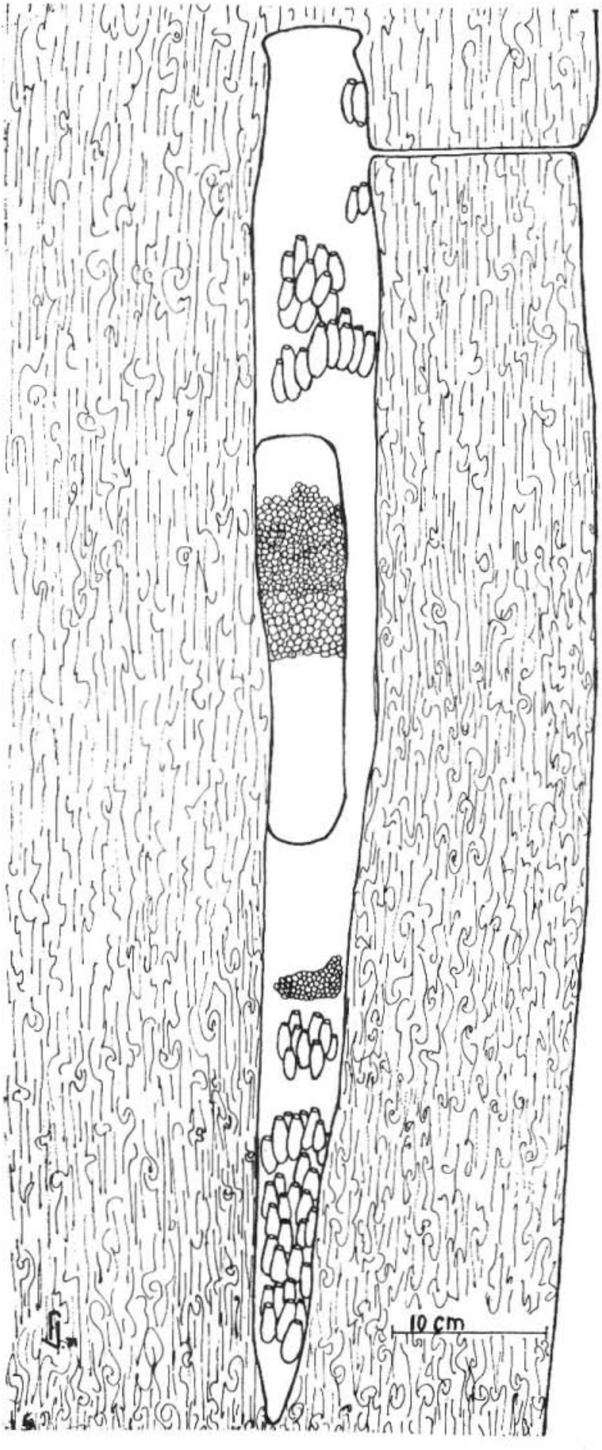
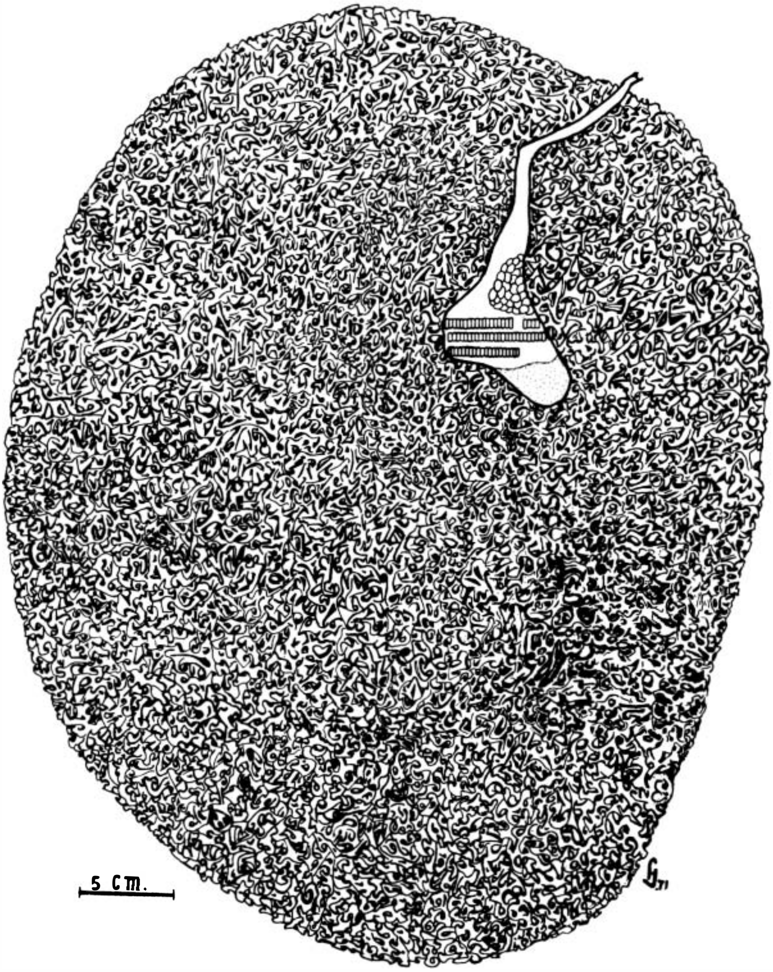


Figure 32. *Trigona (Trigonisca)* sp. B *(sp.* 34), diagram of nest.

Figure 33. *Trigona (Scaura) latitarsis* (*sp.* 35), diagram of nest in *Nasutitermes* nest.

Figure 34. *T. (S.) latitarsis* (*sp.* 35), sectional view of newly made entrance tube on *Nasutitermes* nest, closed for the night by the two bees that spent the night in it. No bee nest was involved; presumably this is an early stage in preparation of a nesting site.



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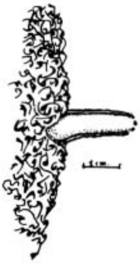

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Figure 35. *T. (Partamona) cupira* (*sp.* 39), nest entrance on earthen bank.

Figure 36. *T. (P.) cupira* (*sp.* 39), nest entrance on a termite nest.

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Figures 37, 38. *T. (P.) cupira* (*sp.* 39), entrance of nest between leaf bases on palm, showing spreading nest material over surface around entrance.


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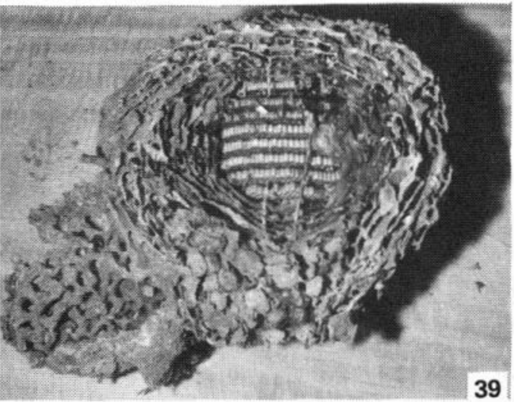
Figures 39–42. *T. (P.) cupira* (sp. 39), nests from near surface of earth bank.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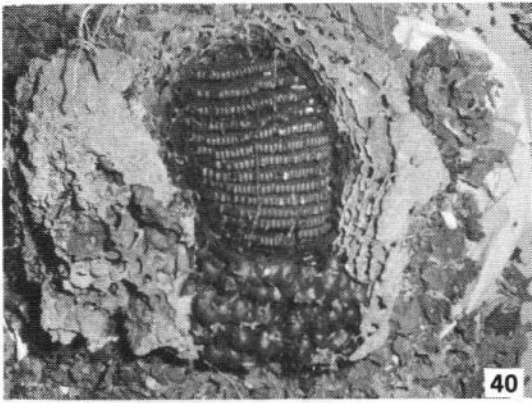
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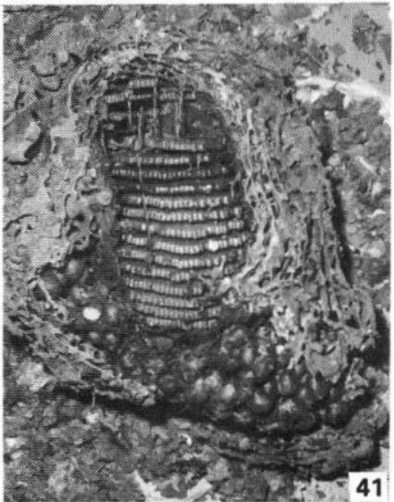
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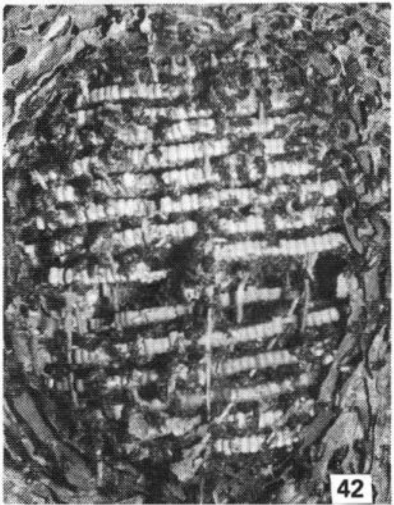
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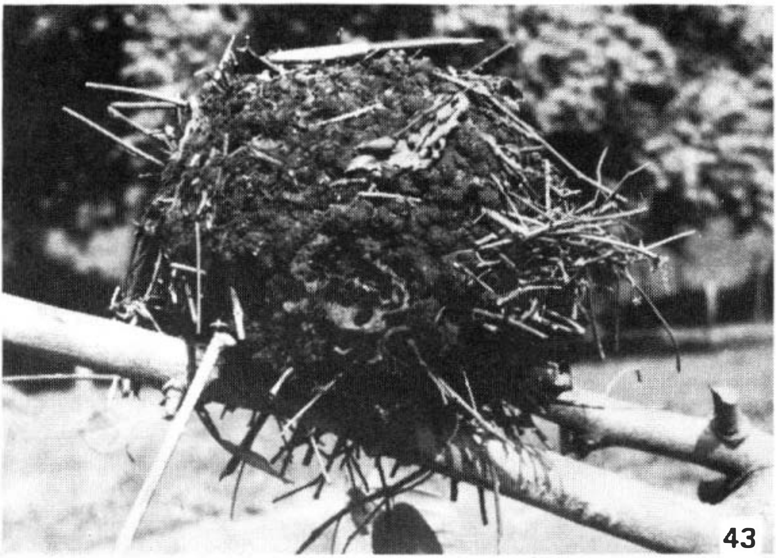
Figures 43, 44. *T. (P.) cupira* (*sp.* 39), nest in abandoned bird's nest in tree.

Figure 45. *T. (P.) cupira* (*sp.* 39), diagrams showing origin of new comb around a permanent pillar. All are top views.



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Cells light yellow–brown, very delicate, axes running in various directions, forming small clusters with no space between cells (fig. 28). Cocoons also pale yellow–brown, tight together (fig. 30), the groups supported by small pillars but individual cocoons in contact or nearly so, almost as in comb–makers but without uniform orientation. Number of cells, 22; number of cocoons, 405.

The cerambycid burrow in which this nest was found was closed at one end by cerambycid feeding frass and at the other end by the vacated cerambycid pupal cell. The bees had done nothing to smooth over these rough materials with cerumen. Their only construction was the internal entrance tube, the pots, and the cells.

The other nest may also have been in an old cerambycid burrow; we saw only a part of the nest which was collected by D.H. Janzen. It differed from the above in lacking an internal entrance tube. The entrance was thick–walled, of blackish material, slightly irregularly projecting. Unlike other nests of the subgenus seen by us, there were hard black batumen plates, 2–8 mm thick. The wood forming the wall of the nest cavity was darkened and in places covered by a visible layer of lining batumen.

34. *Trigona (Trigonisca) sp. B* (fig. 32). Food pots of very thin, transparent, almost cellophane–like material, grouped as shown, 74 in number, 6 with honey, one with pollen, the rest empty. Cluster of cells and cocoons much larger and thicker than in *T. buyssoni*; photographs seem to show varied orientation of cells and cocoons as in that species, as well as groups of adjacent cells and cocoons, while at the same time showing many openings among the cells into which bees can doubtless penetrate. Cells and cocoons mostly in one cluster with advancing front a little above middle; a small separate cluster of cocoons below.

35. *Trigona (Scaura) latitarsis* (figs. 33, 34). Entrance light-yellowish. Batumen only a lining sheet; some sticky material present inside entrance tube where it opens into nest chamber. Pots dark brown, fused but distinguishable. Involucrum absent. Advancing front only at one edge of upper comb, but whole upper comb with eggs. Pillars supporting pots and holding edges of combs to batumen only 1–3 mm long. This may have been a recently established nest, as suggested by the small size of the colony, the few combs, the weak lining of the passageway through the termite nest to the external entrance tube, and possibly by the empty lower part of the nest cavity, closed off from the rest by a thin sheet of cerumen. **Camargo** (9) appears to have described a more mature nest.

The method of establishing a nest in an active termite nest is suggested by figure 34 and by the account of external entrance tubes in a previous part of this paper.

39. *Trigona (Partamona) cupira* (figs. 35 – 45). Entrance broadly funnel shaped, gray, rather brittle, outer margin flaring and irregular, overhanging, upper edge often especially prominent, perhaps as protection against rain; apical diameters shown in Table 5 but throat diameters constricted to 9 to 15 mm. Passage between entrance and nest filled with anastomosing pillars and connectives. When, as in exposed or partly exposed nests, the entrance is close to rest of nest,

this zone very short, passageway being only divided into three or four openings. In nests in soil or whenever entrance is a few centimeters from nest proper, the broad passageway, up to 12 cm in diameter, is filled with the anastomosing, brittle, gray connectives and pillars (fig. 39, lower left). Batumen gray, probably containing earth, rather weak, brittle. several to many layered as shown in illustrations except that in two nests there was an area where it was only one thick layer. Lamina of batumen mostly 1–3 mm thick. Gray earth or batumen material often spread on substrate around entrance (fig. 37) and at one nest forming large sac–shaped pockets on earth bank, several below and one above entrance; when broken, these pockets emitted numerous bees. Involucrum mostly soft, brown, in some nests dark brown, usually several layers thick but sometimes, in some areas of the nest, only one sheet, merging with batumen layers; sometimes a single sheet is soft and brown in one area and becomes hard and gray a few centimeters away. Total thickness of enveloping sheets, where laminate (which is everywhere in most nests), 2–9 cm. Pots dark brown, rather thick–walled and firm, below brood chamber, rarely extending a little up one side, fused and forming a solid mass but individual pots clearly recognizable. Brood chamber with the usual slender pillars of the subgenus, well shown in fig. 41 since that nest had an unusually large space above advancing front; advancing fronts involve two to four combs with advancing edges. Cells dark brown, cocoons light brown.

An unusual nest was constructed in a bird's nest at Playón de Aguirre and had pieces of the bird's nesting material projecting all around; otherwise it was exposed (fig. 43). It contained only a few food pots, nearly all isolated from one another and scattered among layers all around the brood chamber.

New combs are started by a cell attached to the side of a permanent pillar. Other cells are then attached to the first, forming a little group, at first at one side of the pillar, then spreading around it and usually leaving a hole through the comb beside the pillar; figure 45 shows the sequence.

In three nests two or three pots were found that contained mixed pollen and honey. In one case two such pots were at the base of the brood chamber, inside the involucrum, although all other pots were outside, in the normal location.

In one nest (as well as in the nest of *testacea* described below) the batumen sheets in the bottom part of the nest were thickened by deposits of waste and earthen material, and similar deposits were at the back of another nest, seemingly between the outermost layer of batumen and the soil.

42. *Trigona (Partamona) testacea musarum* (figs. 46, 47). Nest agrees with that of *T. cupira* in every respect except anticipated individual differences; it was in an arboreal bird's nest like one unusual nest of *cupira*, and like that nest, had few pots, but they were at the bottom as usual. Entrance at end of projection about 10 cm long and 12 cm in diameter (shown damaged at left in figure 47) full of anastomosing pillars and connectives, inner ends of several connectives end bluntly, directed toward center of nest. Wall of projection hard, 5–10 mm thick, but elsewhere outer batumen layer only 1–2 mm thick, thinner than some of inner layers.

45. *Trigona (Paratrigona) guatemalensis* (figs. 48 – 51). Nest in partial shade

Figures 46, 47. *Trigona (Partamona) testacea musarum* (*sp.* 42), nest in abandoned bird's nest in tree. In fig. 47, the entrance was at the left hand extremity.

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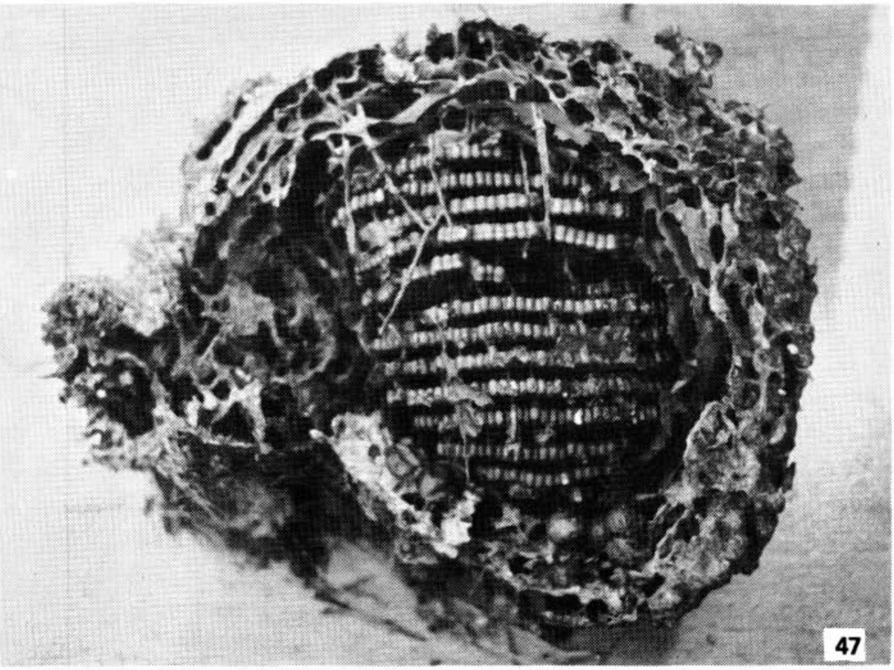

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Figures 48, 49. *Trigona (Paratrigona) guatemalensis* (*sp.* 45), views of nest.

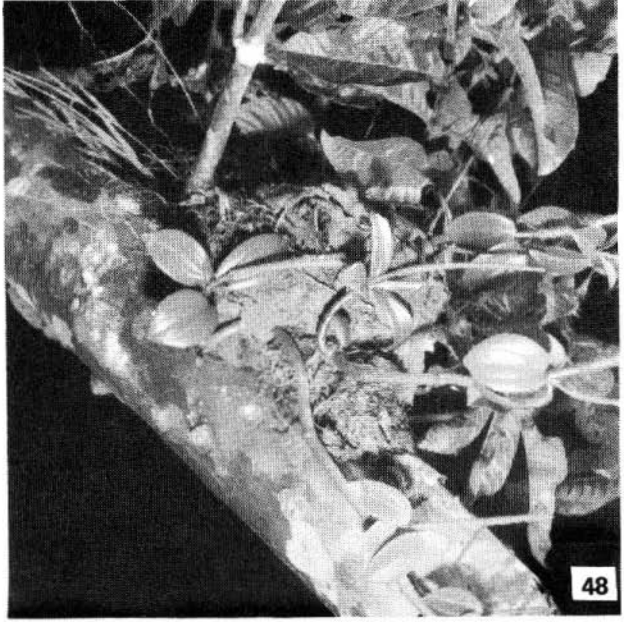
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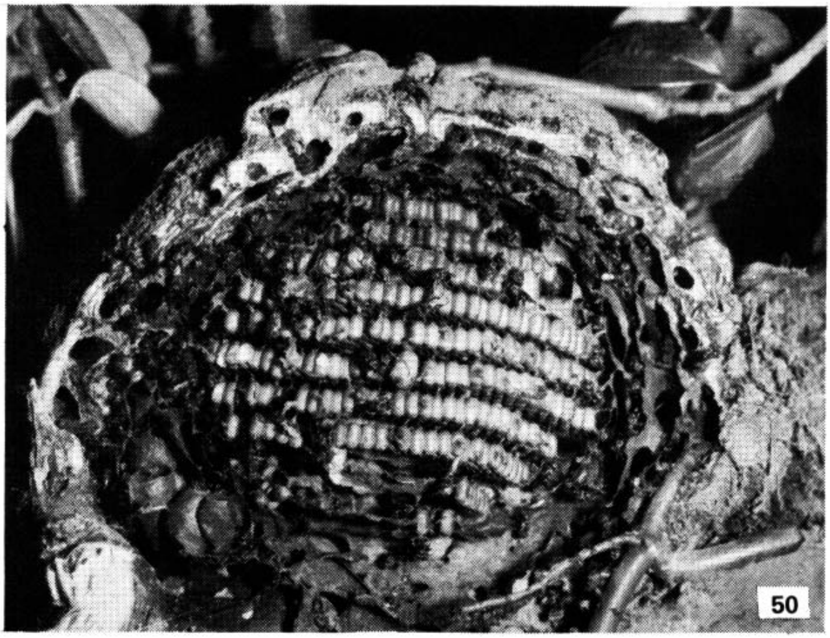
Figure 50. *T. (P.) guatemalensis* (*sp.* 45), nest, opened. Note food pots in lower left.

Figure 51. *T. (P.) guatemalensis* (*sp.* 45), diagram of section through brood combs showing how hollow in combs at bottom is filled in with horizontal sheets which support the new comb.



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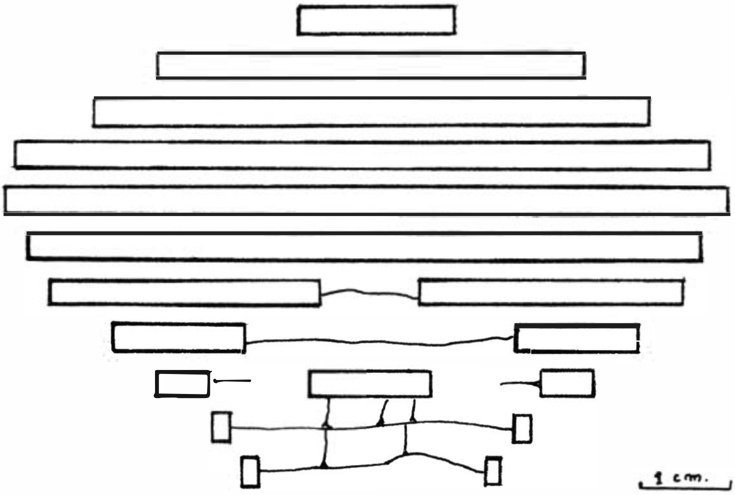

51

Figures 52–54. *Trigona (Paratrigona) peltata peltata* (*sp.* 51). Nests of the ant *Camponotus senex* containing nests of the bees. Entrances of bee nests marked with arrows.

Figure 55. Sectional view of the *Camponotus* nest.


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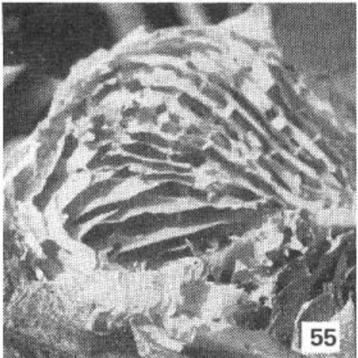
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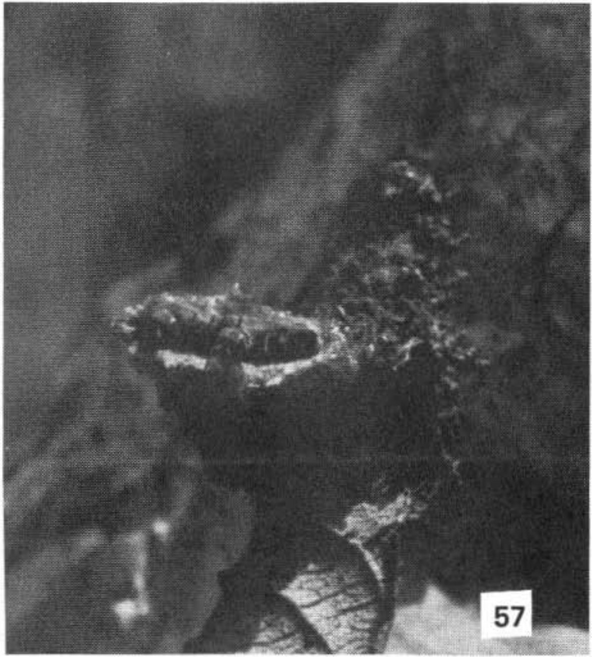
Figures 56, 57. *T. (P.) p. peltata* (*sp.* 51), nest entrances.

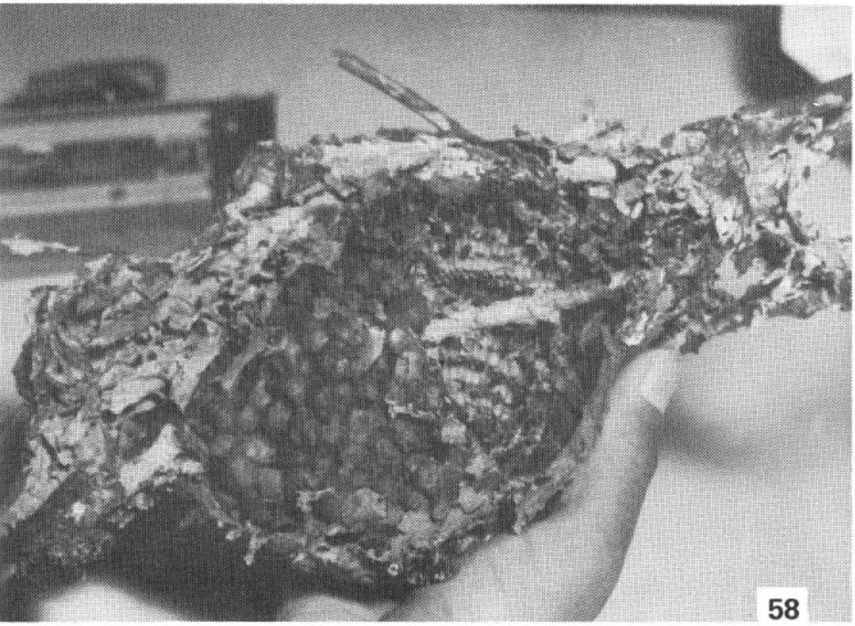
56



57

Figure 58. *T. (P.) p. peltata* (*sp.* 51), nest in *Camponotus* nest.

Figure 59. *T. (P.) p. peltata* (*sp.* 51), diagram of nest in *Camponotus* nest.



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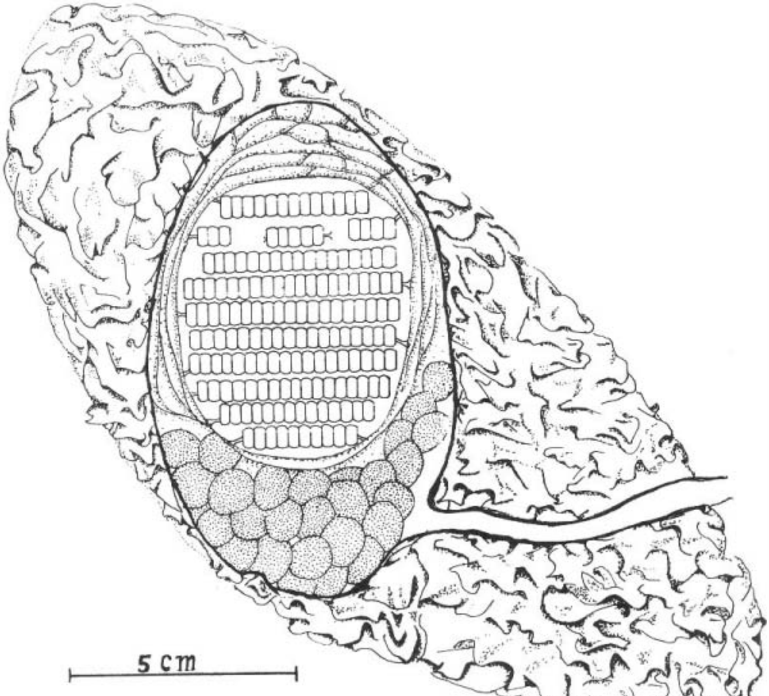
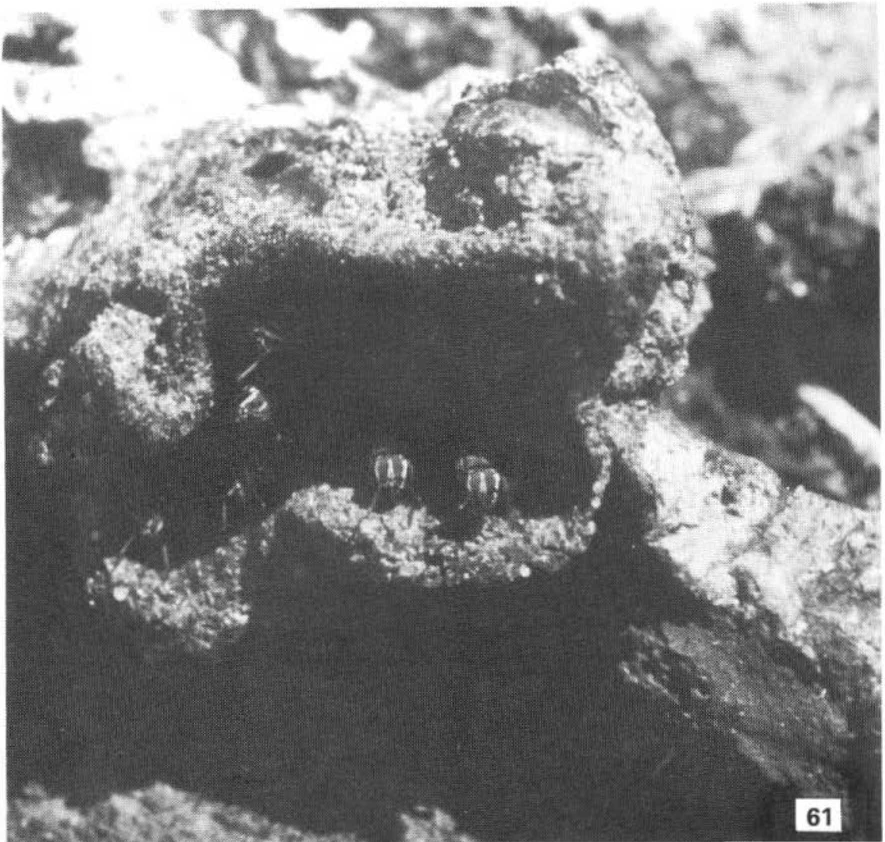


59

Figure 60. *Trigona (Paratrigona) ornaticeps* (*sp.* 49), nest location in rotten *Cecropia* logs.

Figure 61. *T. (P.– ornaticeps* (*sp.* 49), nest entrance.

60



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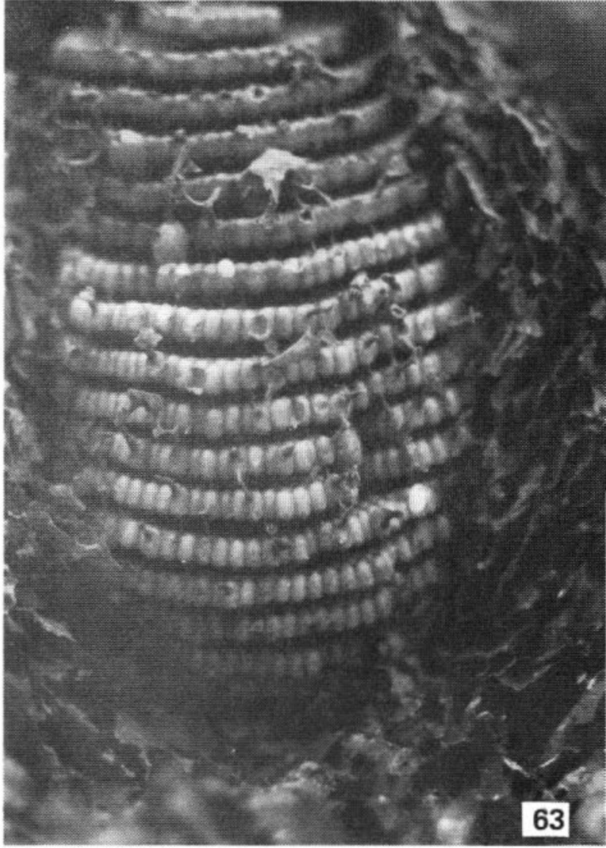
Figures 62, 63. *T. (P.) ornaticeps* (*sp.* 49), interior of nest showing slanting combs.

62



63

on top of slanting branch, with epiphytes on and around it. Entrance projecting, vertically compressed, apex flaring so that measured at margin it is 9 x 21 mm but inside height in throat only 5 mm; margin very thin, soft, flexible, pale brown, with a few small perforations. Exposed batumen on outer and inner surface grayish to red-brown, looking like a mass of mud, very hard, wood-like in texture, not brittle, 10-15 mm thick with passageways in it so that it could be called laminate with layers and connections greatly thickened; bees in most of passageways but ants in a few near entrance; broken surfaces of batumen pale, often greenish; on surface of branch only thin, dark brown lining batumen. Food pots 15, joined in one mass but individual pots perfectly distinct, in lower corner of nest, separated from brood chamber by two layers of involucrum. Involucrum 7-12 mm thick, outer layers dark brown, inner ones pale brown. Cells brown, cocoons light brown. Advancing front at bottom in center, where central openings among old cocoons have been filled with horizontal layers of involucrum-like material, one of which supports the new front (fig. 51). Advancing front on only one comb, space for which is made by removing involucrum-like layer; numerous short pillars between combs of cocoons as well as those of cells. Queen cocoons 6, at margins of combs.

49. *Trigona (Paratrigona) ornaticeps* (figs. 60 – 63). Nest in rotting log that had been down at least two years. Entrance material thick, irregular, blackish; entrance near middle of brood chamber. Thin dark lining batumen and two batumen plates present. From these, long pillars and connections support groups of pots and dense, many-layered, almost cellular involucrum which has a thickness of 2 cm (at right of fig. 62) to 8 cm (upper left of fig. 62); outer sheets of involucrum brownish-black, inner ones brown, all thin, about 0.2 mm thick, flexible, outer ones in particular, slightly brittle. Food pots dark brown, thin-walled, fused in groups but individual pots readily recognizable, located above, below, and at each end of the nest, attached to the outside of the involucrum with some pillars extending to batumen; honey pots 80, in three groups; pollen pots about 60, in one group. Combs all sloping, about 30° from horizontal, but otherwise normal looking. Advancing front at top, involving 5 combs; bottom 5 combs with holes in centers due to emergence of bees; as in other *Paratrigona* these holes closed by transverse lamellae, one for each comb; except for the oldest, combs of cocoons have short pillars between them as do those of cells; queen cells 12, on margins of combs.

It would be interesting to know if the sloping combs are a result of either the shape of the cavity or the tree being down. It is not known whether the bees inhabited this tree before it was felled.

51. *Trigona (Paratrigona) peltata peltata* (figs. 52–59). In our experience this species nests principally in occupied nests of *Camponotus senex* but it has been recorded in a nest of *Dolichoderus*, another ant (63). The arboreal nests of *Camponotus senex* are made of delicate sheets of silk secreted by the ant larvae, plus leaves that become included. The aspect of nests is shown in figures 52 to 54, the internal structure in fig. 55. Some bee nests are found without the associated ants, in nests that are exposed except for some adherent leaves. Some

such nests are probably ones that survive after death of the ants and destruction of their nest. Others may be bee nests made in clumps of leaves without the *Camponotus* or possibly they may have originated with other ants. The long, exposed entrance tubes of bees' nests without ants, however, suggest that they were make in ants' nests or something similar, with the usual short exposed entrance, and that later the substrate (ant nest or ?) disappeared, leaving a much longer exposed tube. The external tube of nests with ants did not exceed 35 mm in length.

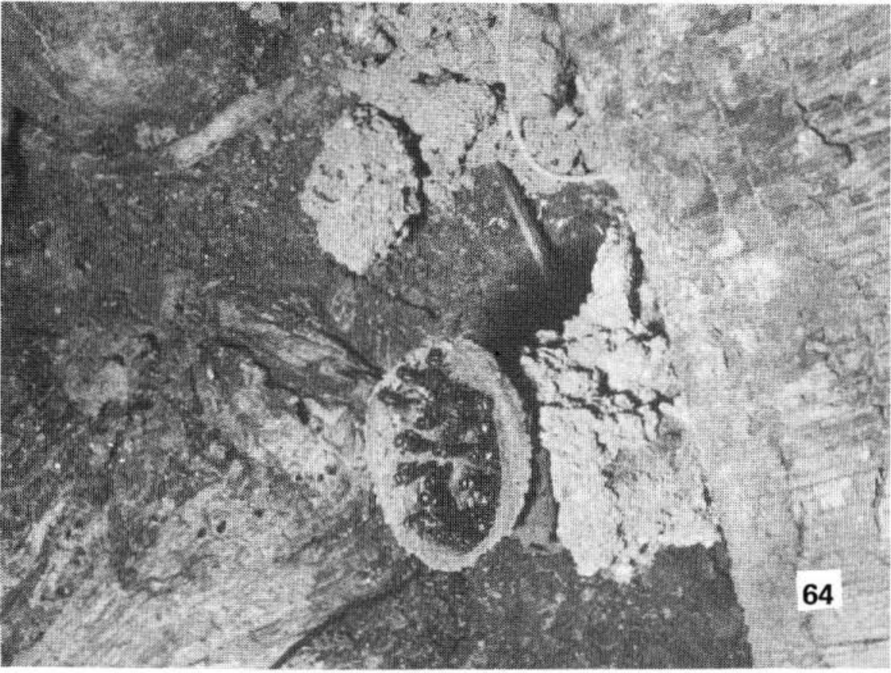
Entrance tube dark gray–brown, often vertically (i.e., dorsoventrally) flattened, with dots of sticky black material (in which ants get caught) on outside, apex often slightly flared, extreme apex pale and minutely irregular, whole tube and especially apex soft. Batumen of one layer, gray to black, rather soft, only about one third millimeter thick. Food pots light–brown, walls very thin and weak, about one third millimeter thick, pots compressed into a single group but lines between them on outside of group perfectly plain. Pots located under brood if there are few (6 or 8), extending as solid mass up one side if there are many (70). Involucrum of very thin, light–brown, soft sheets, in some areas of only one layer but in most parts of most nests two to five. Cells brown, cocoons light brown. As in *T. guatemalensis*, space above an advancing front is filled with usually horizontal laminae, the advancing front is limited to one comb, and numerous short pillars connect both combs of cocoons and those of cells. Queen cells mostly but not all on margins of combs.

Sometimes, as in figure 58, a twig through the brood chamber makes for some irregularities. This figure shows the pots mostly to the side of the brood chamber, as is sometimes the case, in contrast to beneath it as in. figure 59.

55. *Trigona (Scaptotrigona) mexicana subobscuripennis* (figs. 64 – 68). Entrance quite variable, sometimes funnel–shaped, narrowed at throat to 12–30 mm in diameter, but sometimes almost cylindrical, or rather irregular and without a projecting tube; edge when projecting thin, yellowish–gray, or gray brown, soft, slightly irregular, sometimes perforated; very dense material sometimes used to narrow a large natural opening (10 cm in diameter) to the proper size. Internal entrance tube 3–4 cm long, extending straight in from entrance. Lining batumen brownish- black. Unused space in box nest filled with numerous dark brown papery sheets but little or no such material in natural nests. A few pillars and connectives supporting storage pots, which were at one side and beneath brood chamber in box, above it in natural nest, lateral to it in horizontal nest; walls of pots 0.5–3 mm thick, outer wall of each group thickened with added cerumen, individual pots scarcely distinguishable. Involucrum of three or six thin papery sheets all around brood chamber, total thickness 1.5–4 cm, paler brown than space--filling sheets. Advancing front involved 2 combs, cavity above front partly filled with small sheets and pillars in one nest; in figure 1 of the outside of the combs, oldest cocoons are at bottom and combs of cells at top.

A nest in a large piece of bamboo that had been horizontal contained two sets of combs side by side in a single brood chamber. The vertical diameter of the bamboo stem available to this colony was only 8 cm, insufficient for a normal brood chamber.

Figures 64, 65. *Trigona (Scaptotrigona) mexicana subobscuripennis* (*sp.* 55), nest entrance.



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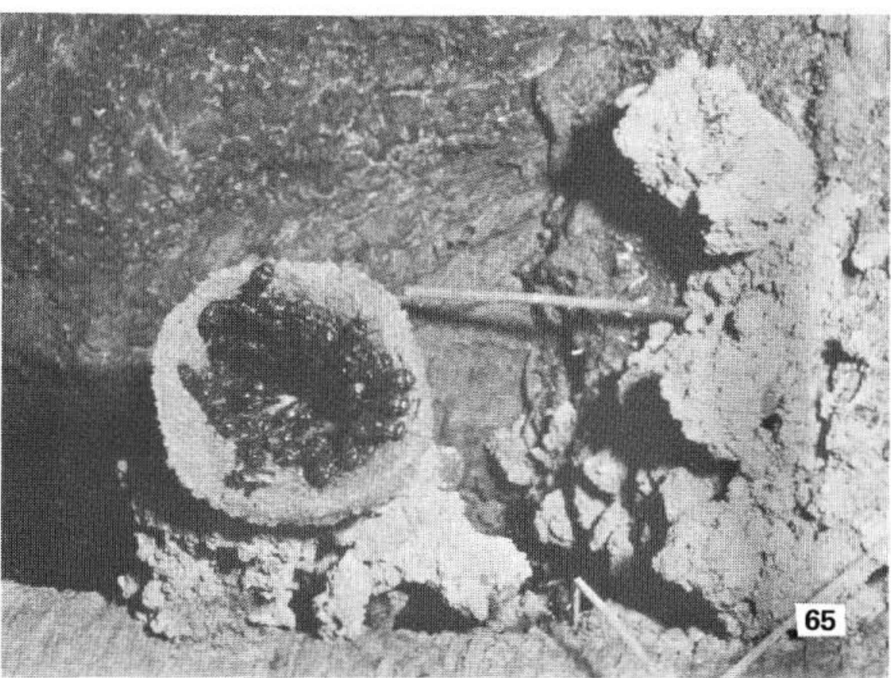
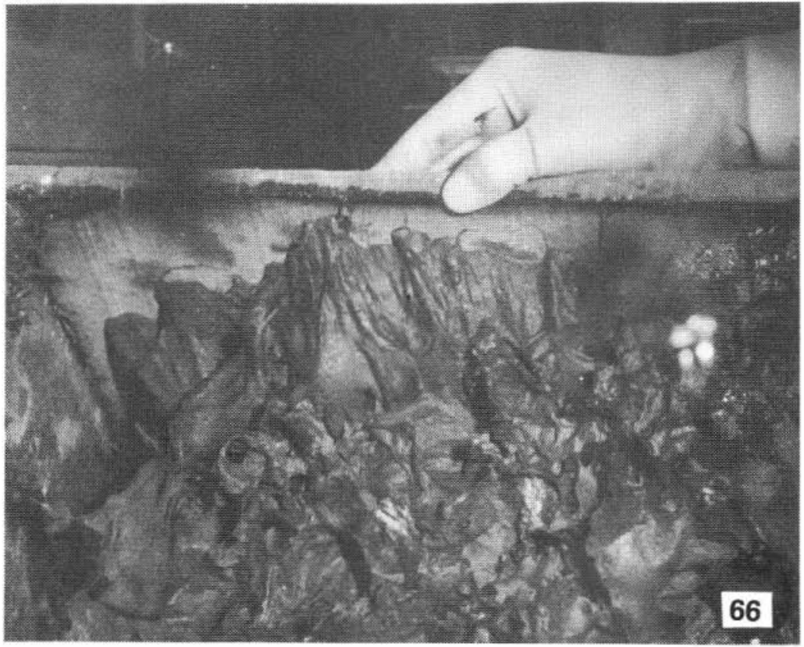


65

Figure 66. *T. (S.) m. subobscuripennis* (*sp.* 55), sheets of material filling a box in which William Ramírez B. kept a colony.

Figure 67. *T. (S.) m. subobscuripennis* (*sp.* 55), brood chamber surrounded by laminate involucrum.



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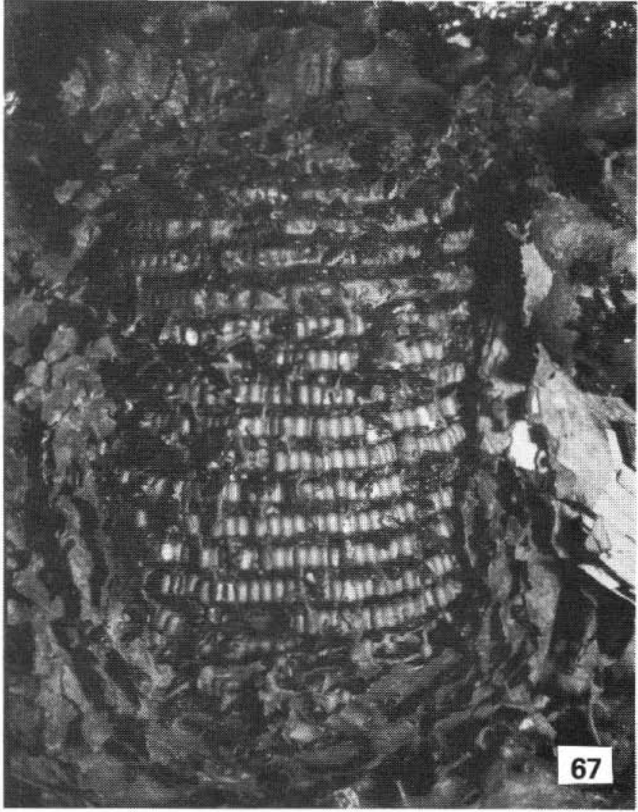

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Figure 68. *T. (S.) m. subobscuripennis* (*sp.* 55), vertical section through nest.

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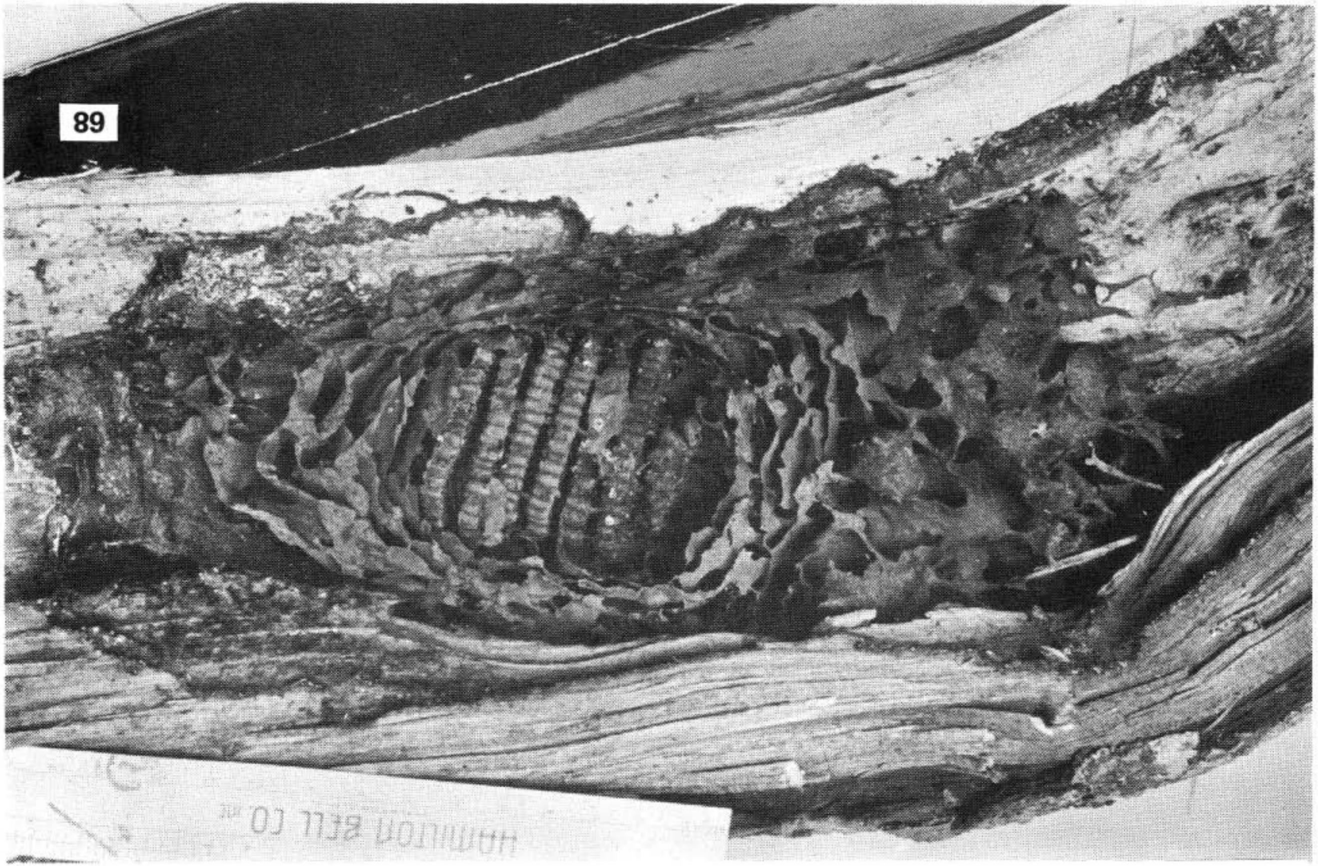
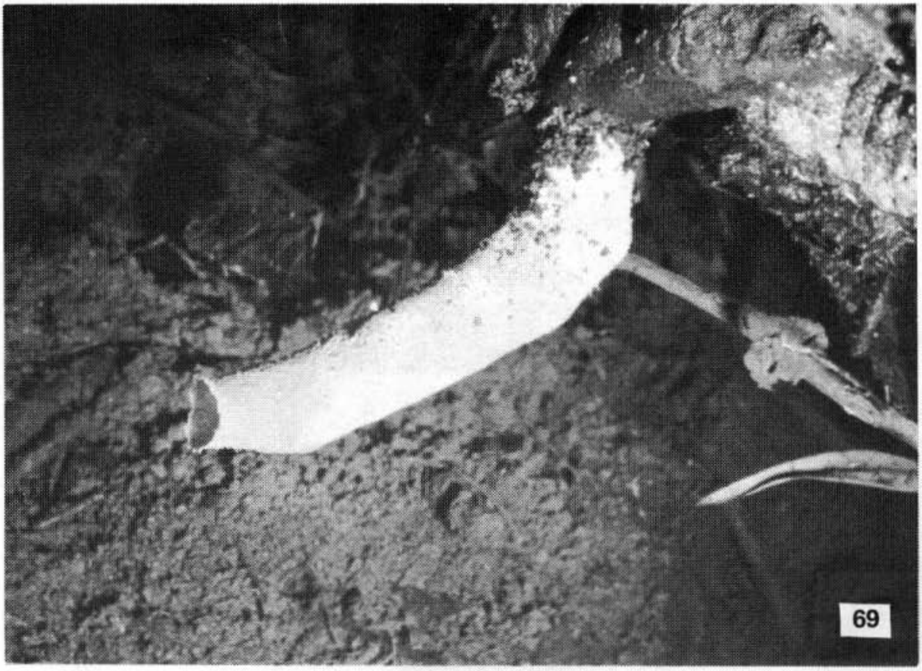


Figures 69, 69a. *Trigona (Nannotrigona) mellaria* (sp. 61), nest entrances.



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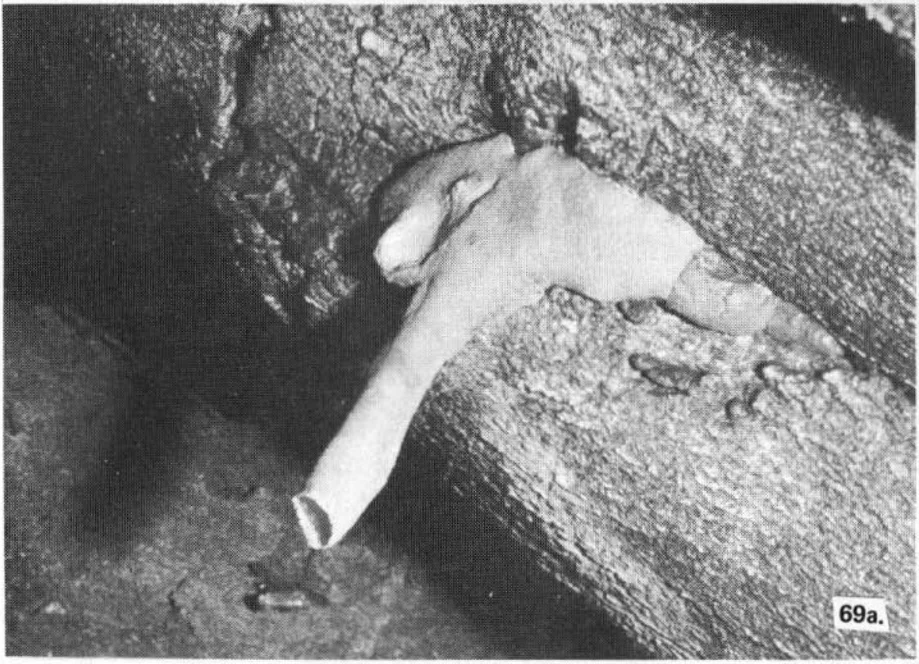
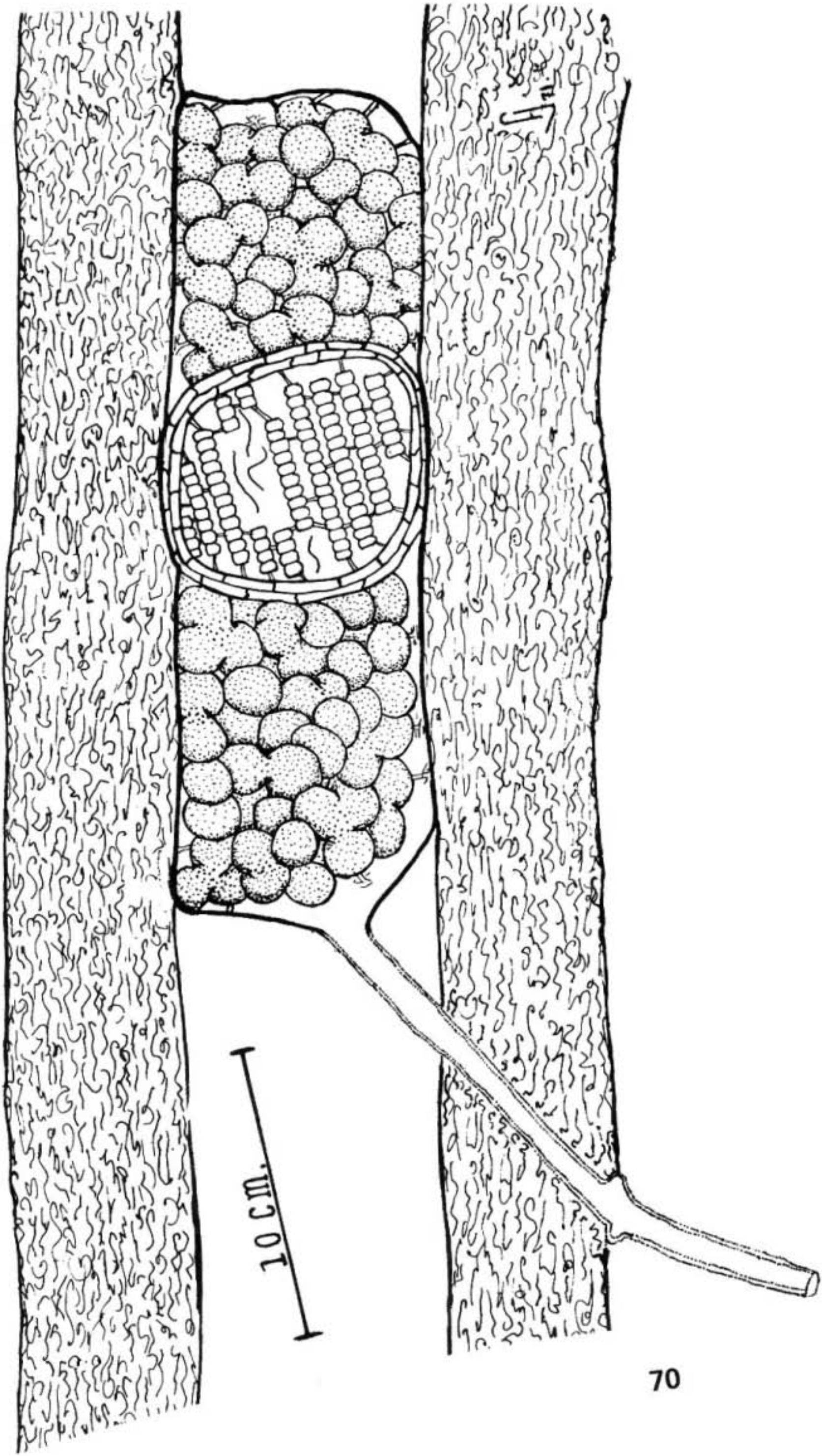


69a.

Figure 70. *T. (N.) mellaria (sp.* 61), diagram of nest.

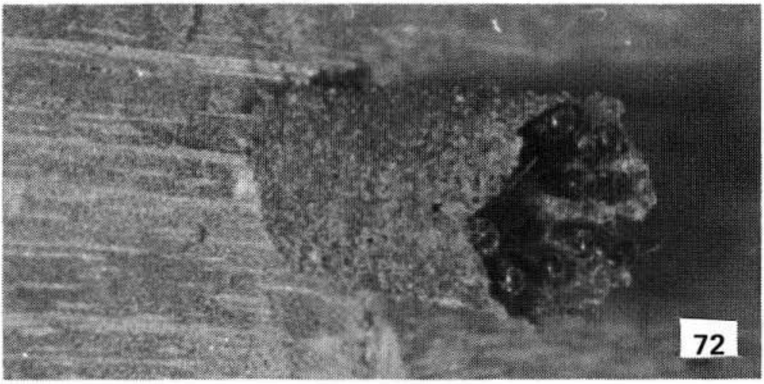


70

Figure 71. *Trigona (Nannotrigona) testaceicornis perilampoides* (*sp.* 62), short external entrance tube.

Figures 72, 73. *T. (N.) t. perilampoides* (*sp.* 62), ordinary sized external entrance tube of nest kept in a box, in fig. 73 closed for the night.

71



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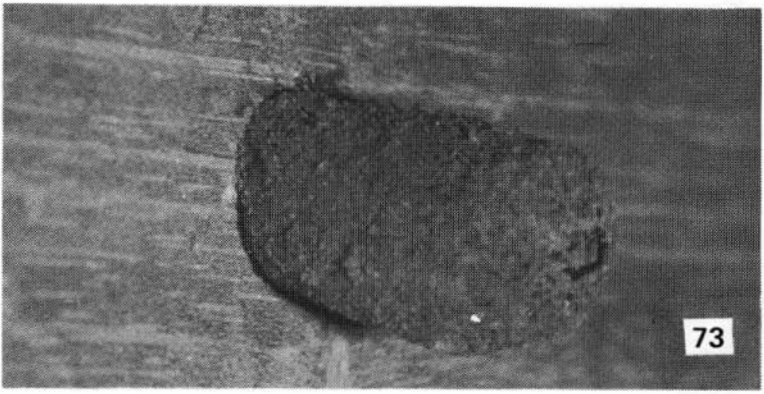

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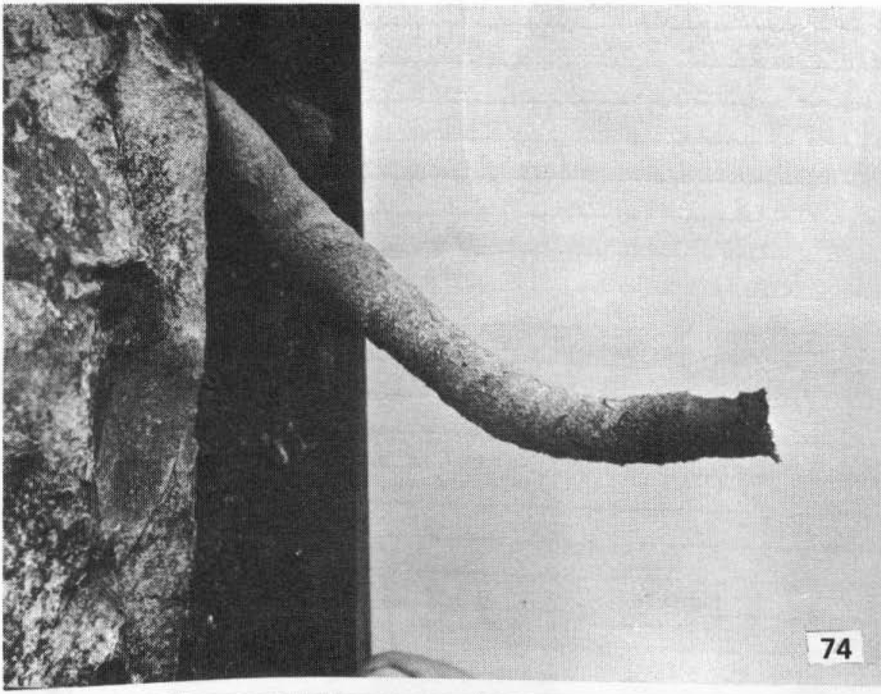
Figures 74, 74a. *T. (N.) t. perilampoides* (*sp.* 62), extraordinarily long entrance tube of nest projecting from wall of ruins at Old Panama.



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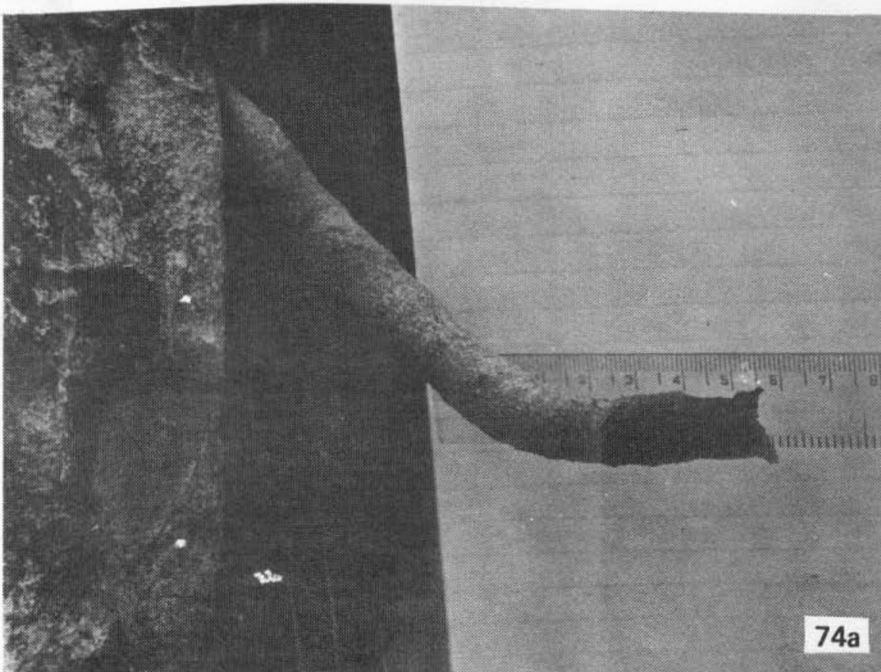
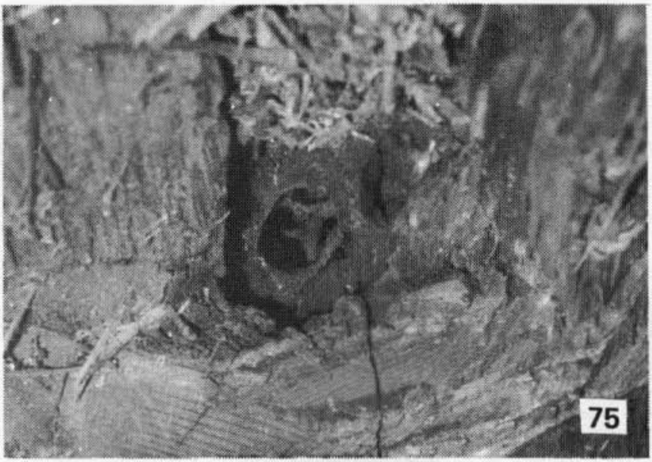


74a

Figure 75. *T. (N.) t. perilampoides* (*sp.* 62). Removal of entrance tube show pillars and connectives inside.

Figure 76. *T. (N.) t. perilampoides* (*sp.* 62), pillars and connectives in passage through log to nest; entrance was at left.

Figure 77. *T. (N.) t. perilampoides* (*sp.* 62), pillars and connectives filling space in box where nest was placed; a little brood visible to lower left of center, but expansion of pillars and connectives is producing involucral sheets.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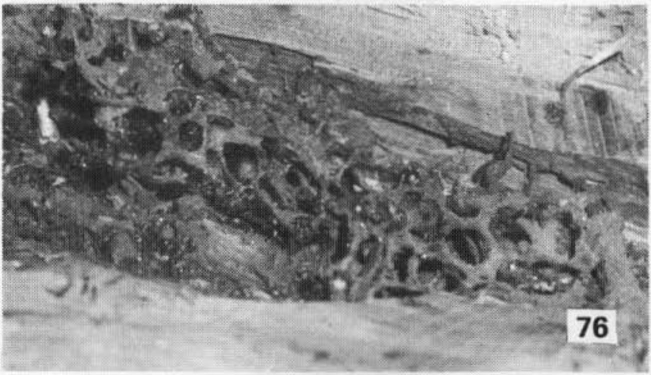
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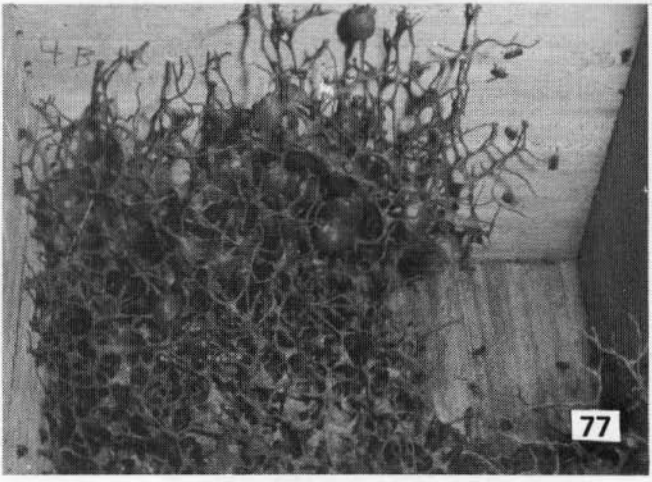

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Figure 78. *Trigona (Cephalotrigona) capitata zexmeniae* (*sp.* 64), diagram of nest.

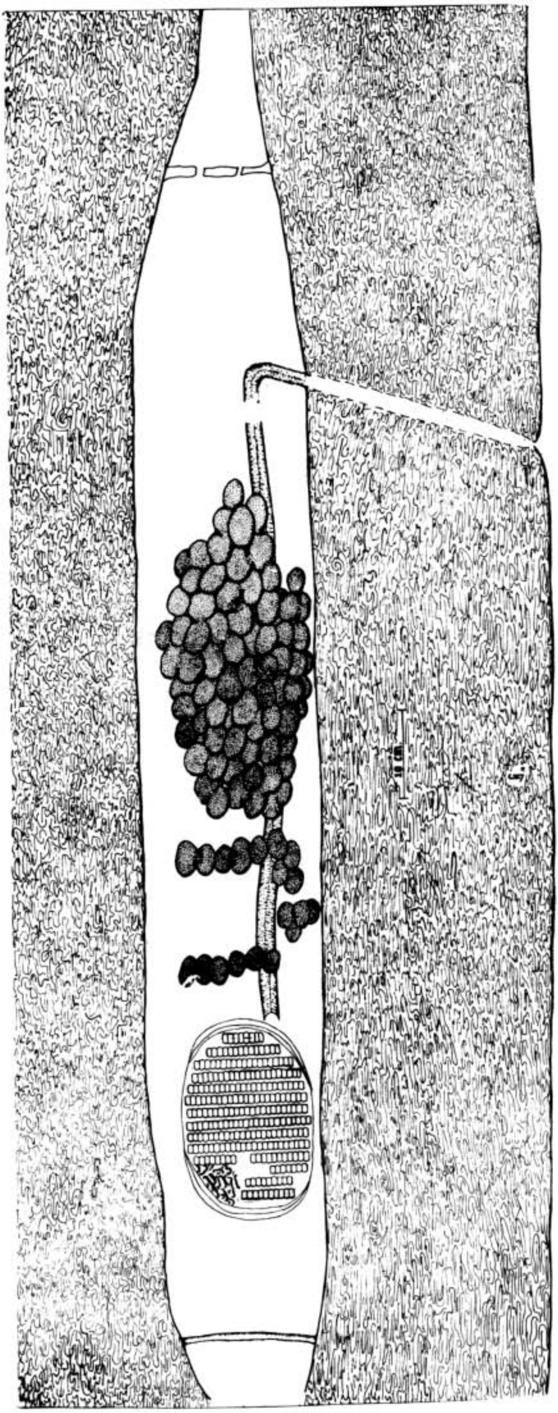

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Figure 79. *Trigona (Oxytrigona) tataira mellicolor* (*sp.* 67), diagram of nest.

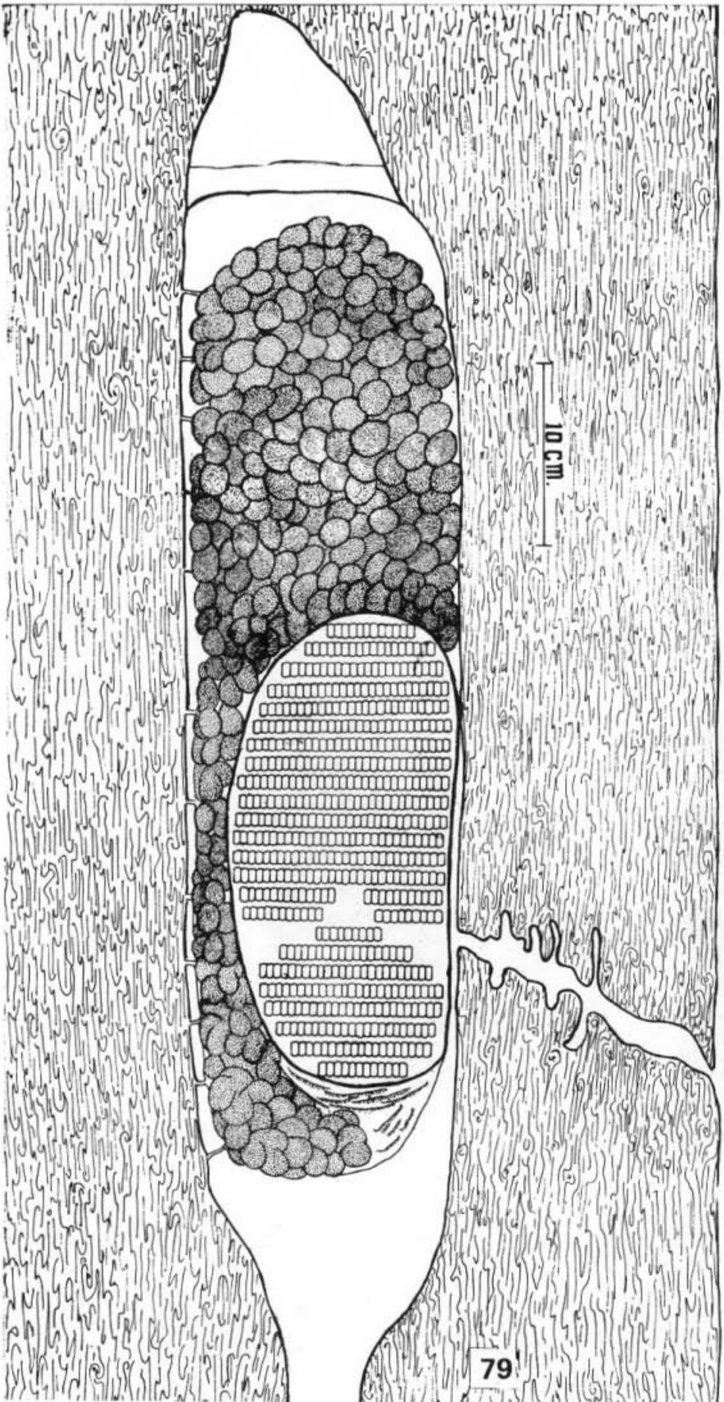

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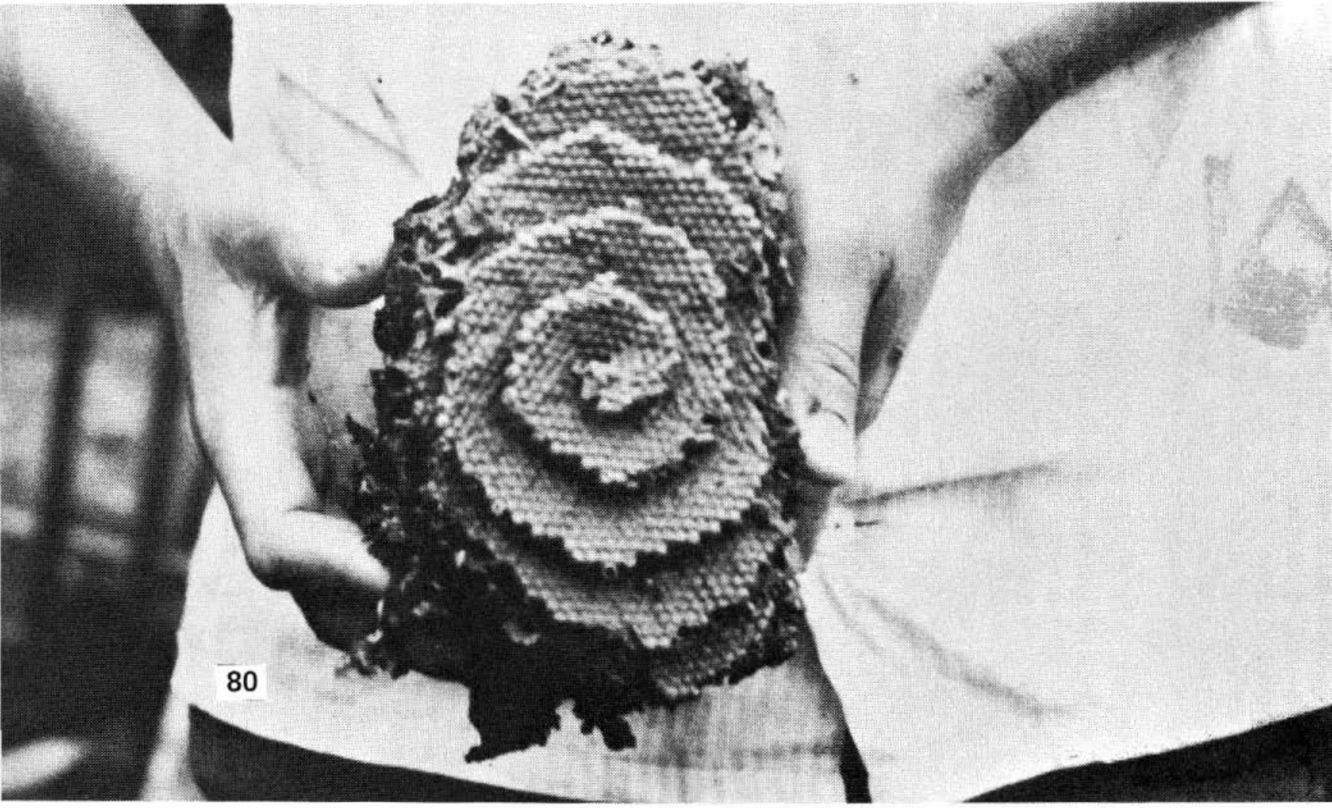
Figure 80. *T. (O.) t. mellicolor* (*sp.* 67), top of brood combs.



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The few nests of this species which we have studied suggest the possibility of two cryptic species being involved. Some are in relatively large colonies, have well formed funnel–shaped entrances narrowed to throat diameters of 20–30 mm, and a brood chamber of about 10 x 16 cm. The other, in smaller colonies, has little or no funnel development at the entrance, throat diameters as small as 12 mm, and brood chambers as small as 5.5 x 7 mm. Age and nest site may account for these differences, but the possibility of specific differences should be considered in the future.

61. *Trigona (Nannotrigona) mellaria* (figs. 69 – 70). Two nests in a hollow tree that had fallen seven or more months before. Entrance tube brownish–tan, darker basally, hollow enlargement at base strong, brittle, walls 1–1.5 mm thick. Batumen black, consisting of strong but flexible plate at each end as well as lining. Rest of nest everywhere separated from batumen by small pillars and connectives 3–3.5 mm long. Food pots dark brown, mostly at each end of nest but some also at sides of brood chamber, no space above or below; pots with walls flexible, soft, very thin; pots tightly packed but individually recognizable from outside. Involucrum of four light brown sheets separated by flattened pillars and connectives about 3 mm long. Cells dark brown, cocoons tan; advancing front in middle of brood chamber, space above it partly filled by involucrum –like sheets.

62. *Trigona (Nannotrigona) testaceicornis perilampoides* (figs. 71 – 77). Entrance tube brown, thin, tattered and irregular at apex, zone of irregular pillars and connectives inside. Nest in large box seems to be filling whole box with anastomosing pillars and connectives (fig. 77) which support pots and even leave part of brood exposed (this exactly as in *T. carbonaria;* **Michener,** 32) as the pillars and connectives are being expanded to form an involucrum. Nests in logs (two studied) showed such pillars only near entrances. Pots were on only one side (toward entrance) of brood chamber in nests in logs.

The only differences between nests of this species and these of *mellaria* are the usually short and darker external entrance tubes, the pillars and connectives inside the entrance (fig. 76), and the presence of only one involucral layer. The latter may be variable.

63. *Trigona (Cephalotrigona) capitata zexmeniae* (fig. 78). Entrance a mere hole formed of cerumen in knot or crevice in tree trunk; internal entrance tube extending 65 cm down through nest cavity. Batumen plates distinct, thin (5 mm or less), black; lining batumen present only in certain areas. Storage pots dark brown, fused but very distinct from outside, all above brood chamber, a group of pollen pots between two groups of honey pots; walls of pots 0.4–0.7 mm thick. Involucrum of one (laterally) to three (above and below) dark brown, soft, irregular sheets. Only one advancing front.

An unusual feature is that brood cells are filled only half full, and the cell contents are firm and rather dry instead of semiliquid as in other forms.

67. *Trigona (Oxytrigona) tataira mellicolor* (figs. 79 – 80). Nest entrance

merely a small irregular hole or two holes, lined with cerumen, in a groove in a tree trunk, part of the groove also lined with cerumen. Passage through wood to nest in one case very irregular with numerous diverticulae lined with cerumen, not closed off. Nest cavity with thick blackish batumen plates and thin blackish lining batumen, a second batumen layer 4 mm inside the first and separated from it by pillars on one side of one nest. Pots dark brown, numerous, fused but distinguishable from outside, large mass above and in one nest below brood chamber and also extending along one or more sides of chamber; pots fused, walls about 1 mm thick, pollen and honey pots intermixed, those above chamber all with pollen in one nest. Involucrum mostly of a single sheet, very incomplete and soft in one nest but with 3–4 layers at bottom, in the other nest complete but of only one layer with lower part hard. Cells dark brown, cocoons light brown; one advancing front involving one or two layers.

71. *Trigona (Tetragona) buchwaldi* (fig. 81). Nest described and illustrated by **Wille** (74). Distinctive features of the subterranean nests are the single batumen layer, the much elongated pots, pollen pots separated from honey pots by a partition of cerumen, and the laminate involucrum.

75. *Trigona (Tetragona) dorsalis* (figs. 82 –85). Nest 1 (north of Quepos). In vertical hollow in base of tree. Exposed entrance tube dark brown, base blackish; length 8 cm, walls hard, thick, perforated in apical 5 cm with rather large holes, up to 1 mm wide and 3 mm long; surface with small protuberances and slender hanging projections up to 17 mm long, some branched, hanging like small roots. Batumen plate at base but not at top of nest cavity, this plate and lining batumen nearly black. Pots below brood chamber with honey as are those innmediately above, but rest of upper cluster with pollen; walls of pots thin, black; pots fused, only moderately distinct on outside. Involucrum of about two layers laterally, four or five above and below, thin, black or inner layer brown, some parts brittle, others soft and flexible; short pillars separate involucrum and pots from batumen. Advancing front at lower third of brood chamber but no new cells being made; perhaps cell construction is synchronized; arrangement a spiral except for uppermost comb which is indepentent; cells heavily coated with cerumen.

Nest 2, Pocares. In horizontal hollow 10 cm below surface of ground under roots of *Cecropia* tree; many small roots passed through nest so that it was broken up in removal. Exposed entrance tube black; length 8 cm; walls 0.75–3 mm thick, perforated throughout length, surface irregular, nodulose, but without root–like projections. Cavity lined with single layer of black batumen, partly strong, partly rather weak and brittle. Pots below brood chamber contained pollen, those above, honey. Other details not observed (except that the comb was spiral) because of roots wich pulled through the nest but fig. 166 gives an approximation of the organization.

Two other nest entrances, 10 and 15 cm long, and both having root–like projections like those of number 1, have also been seen by us.

85. *Trigona (Tetragona) jaty jaty* (figs. 86–100). Although this species never

Figure 81. *Trigona (Tetragona) buchwaldi* (*sp.* 71), diagram of nest.

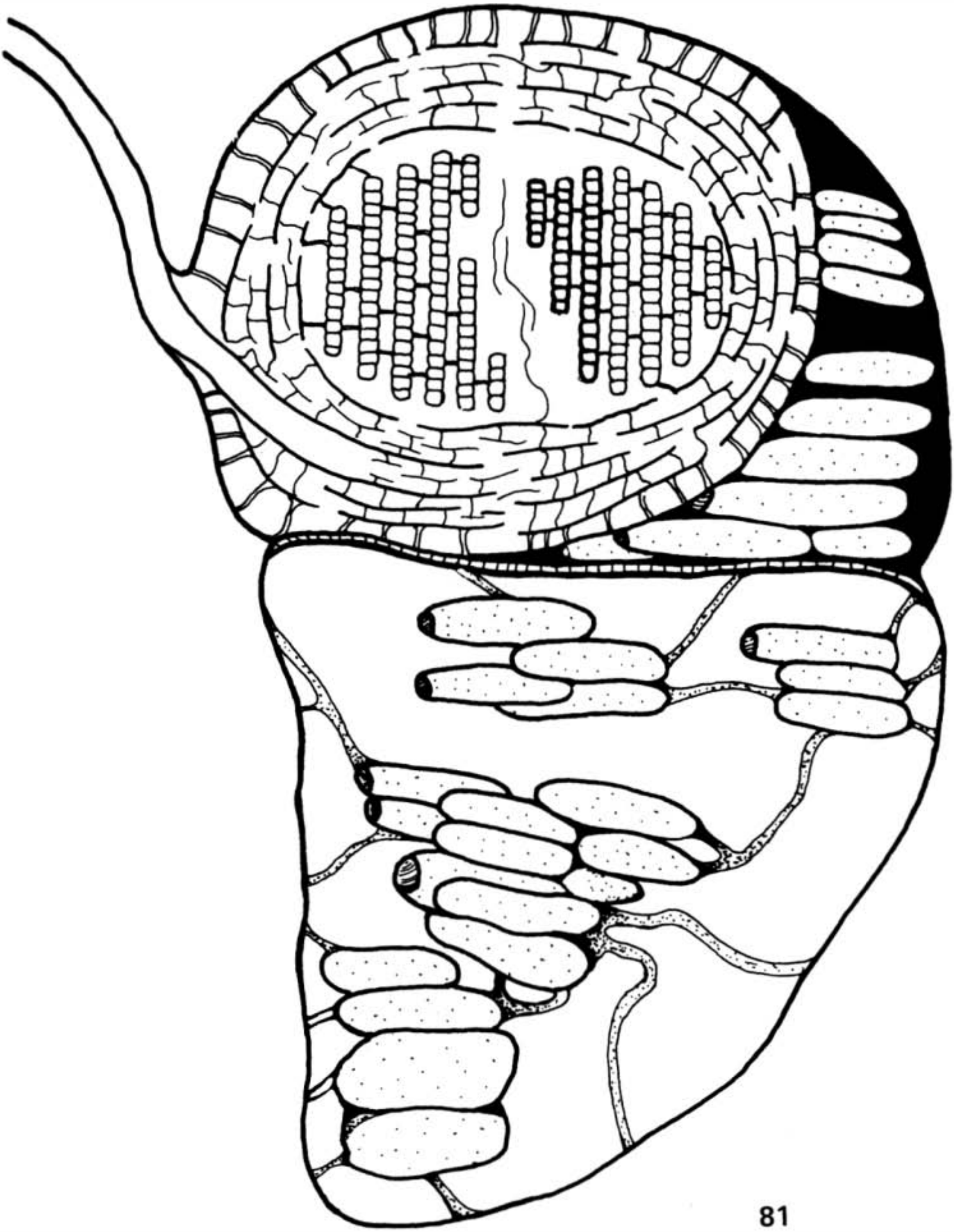

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Figure 82. *Trigona (Tetragona) dorsalis (sp.* 75), diagram of nest.

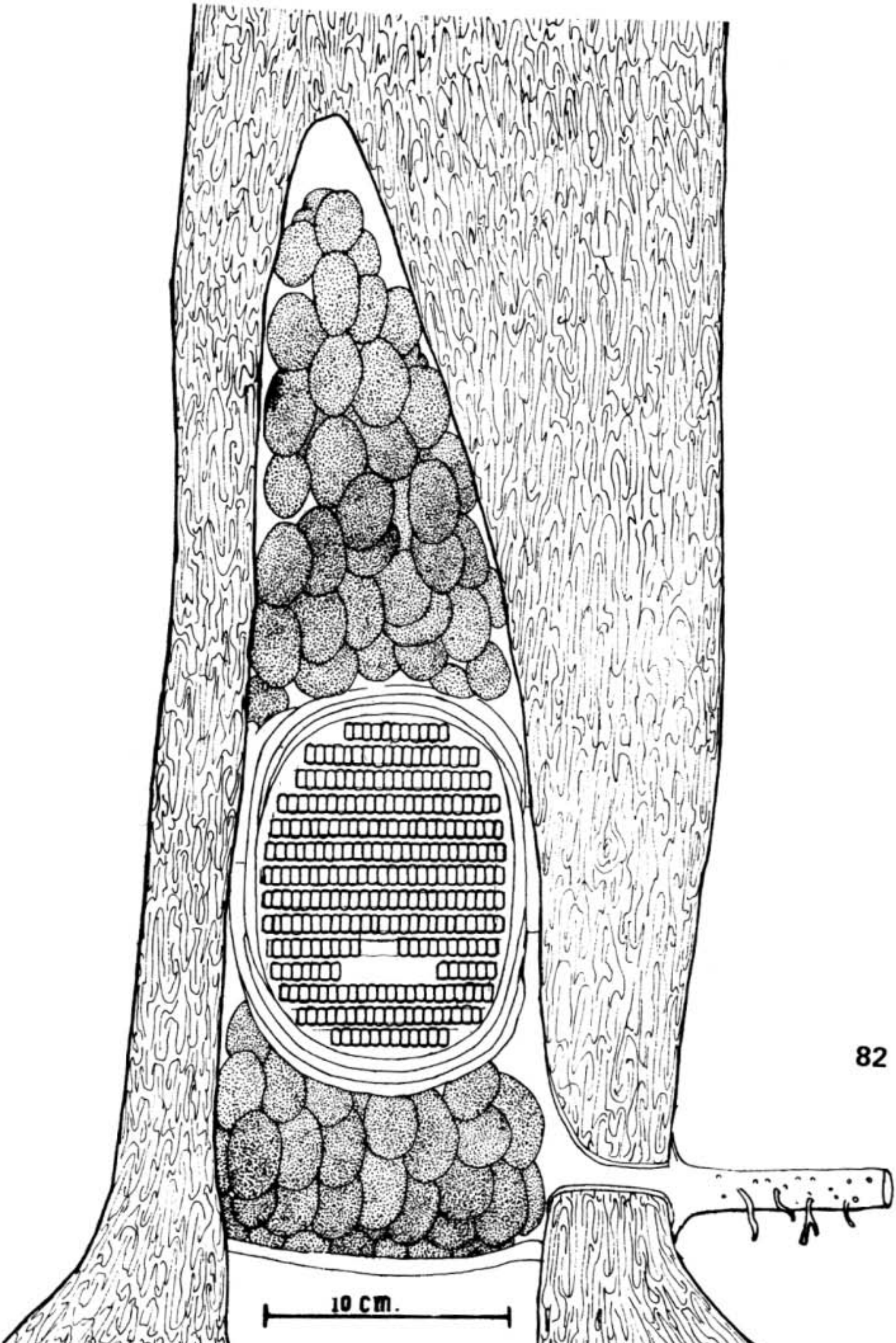

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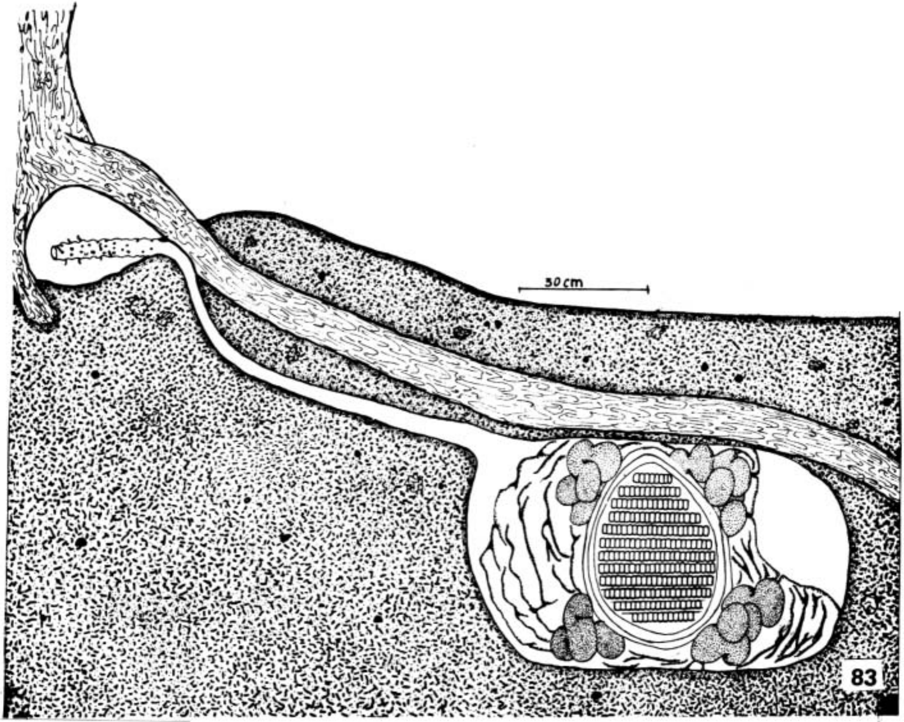
Figure 83. *Trigona (Tetragona)dorsalis (sp. 75)*, diagram of nest.



30 cm
83

Figure 84. *T. (T.) dorsalis* (*sp.* 75) nest cavity opened to show pots and involucrum.

Figure 85. *T. (T.) dorsalis* (*sp.* 75), brood combs.

84

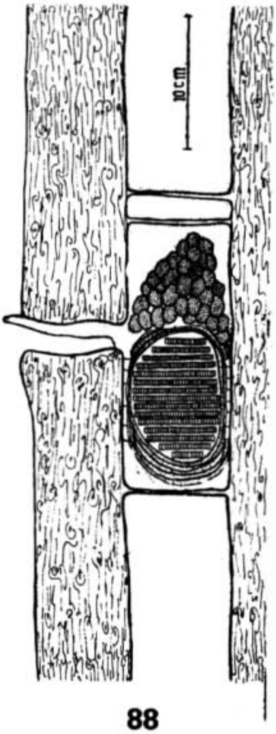
85

Figures 86, 87. *Trigona (Tetragona) jaty jaty* (sp. 85), nest entrance, 86 of usual form but unusually dark, 87 double and pale.

86

87

Figures 88, 89. *T. (T.) j. jaty* (*sp.* 85), diagrams of nests, the latter in unusually long, slender cavity.



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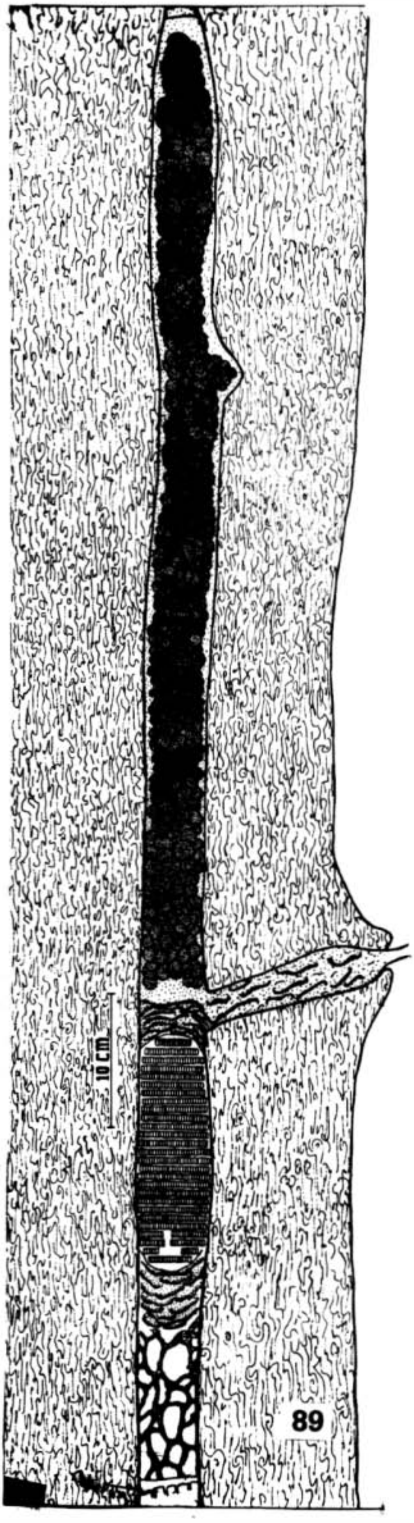

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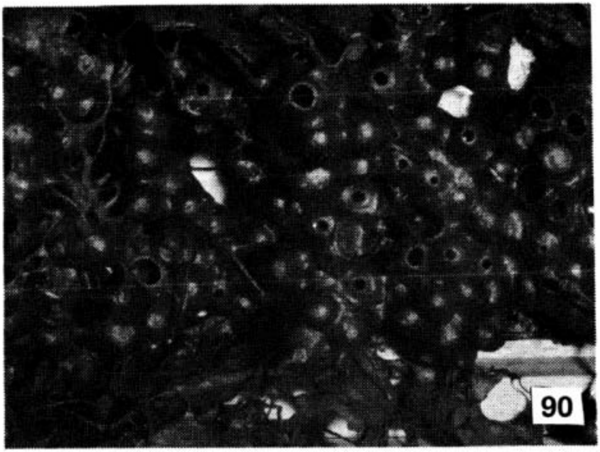
Figure 90. *T. (T.) j. jaty* (*sp.* 85), top view of pots in nest box.

Figures 91, 92. *T. (T.) j. jaty* (*sp.* 85), top and side views of brood combs which were divided vertically. In fig. 91 cells were exposed in left hand group, cocoons in right; in 92 the reverse.



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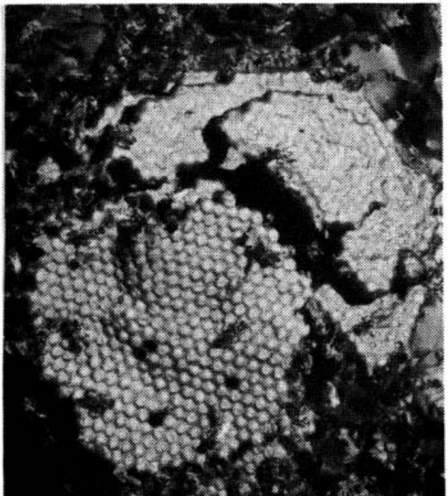

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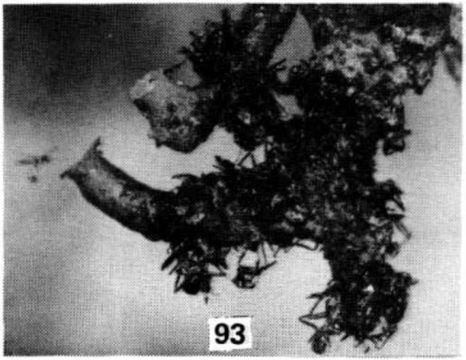
Figures 93–96. *T. (T.) j. jaty* (*sp.* 85), a typical soft yellow entrance tube coated with a thick sticky material, applied by the bees. Stuck to the tube there were 60 workers of *Camponotus silciventris*, an aggressive and omnivorous ant.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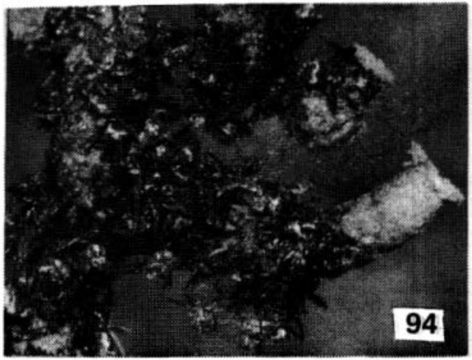
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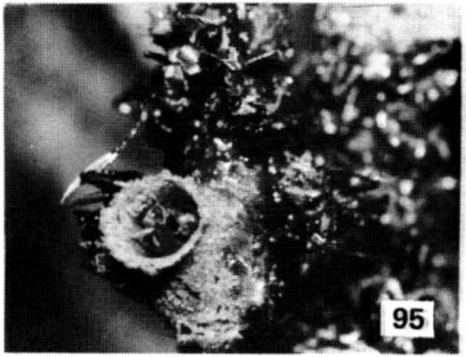
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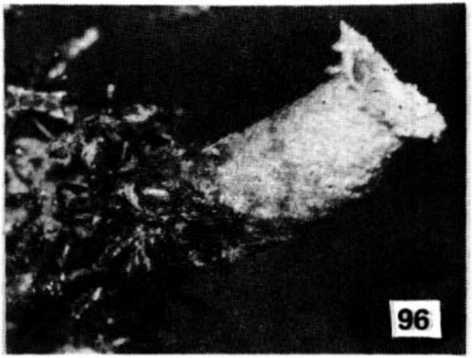
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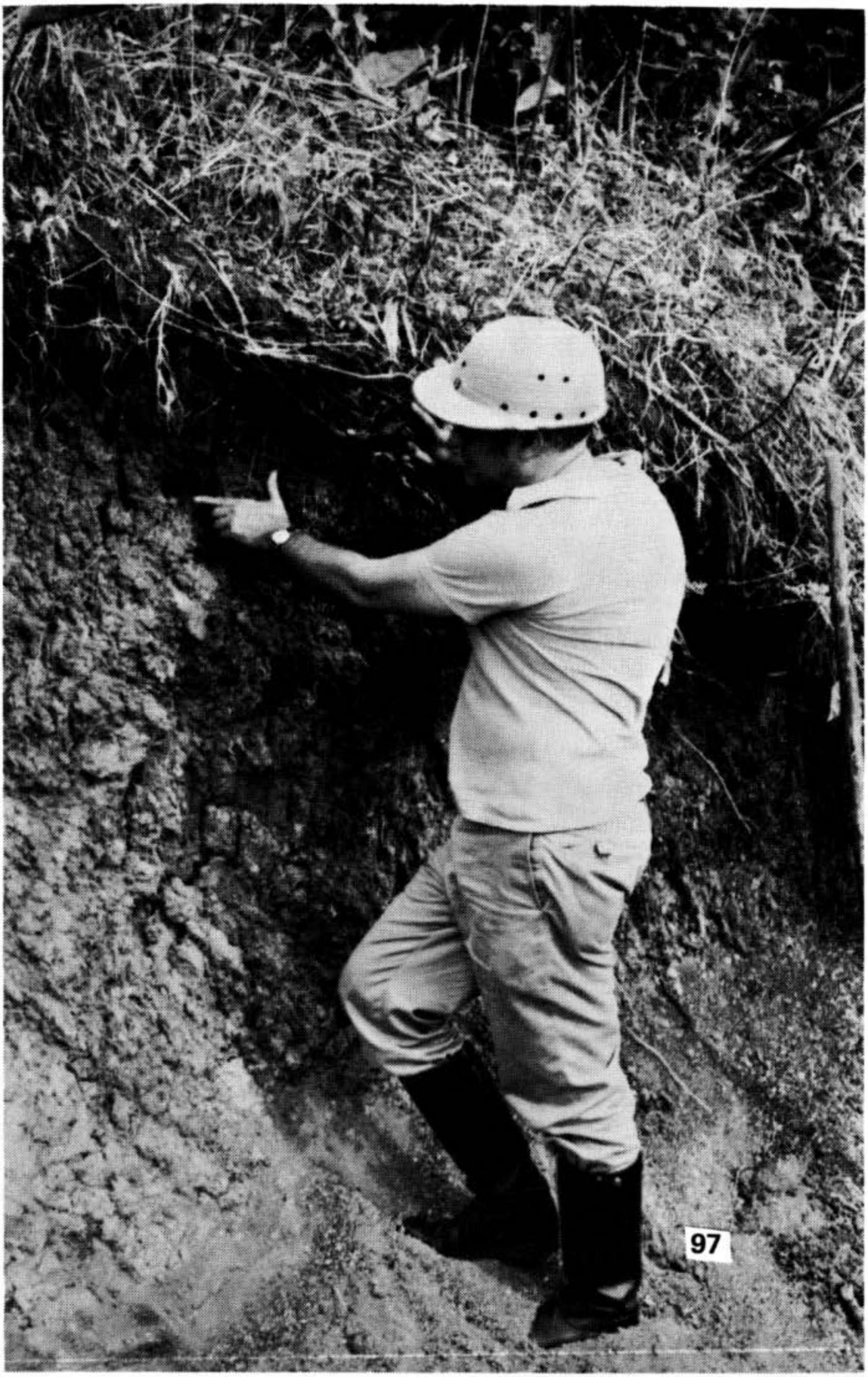
Figure 97. *T. (T.) j. jaty* (*sp.* 85), showing the location of the nest in a road cut.



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Figures 98, 99. *T. (T.) j. jaty* (*sp.* 85), the entrance of the nest found in the ground.

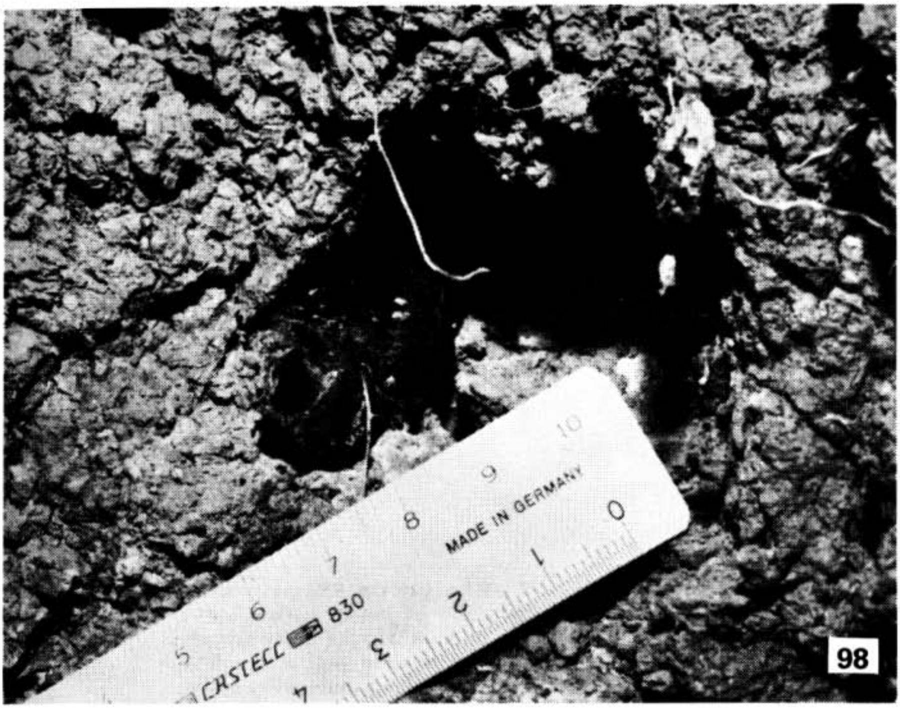

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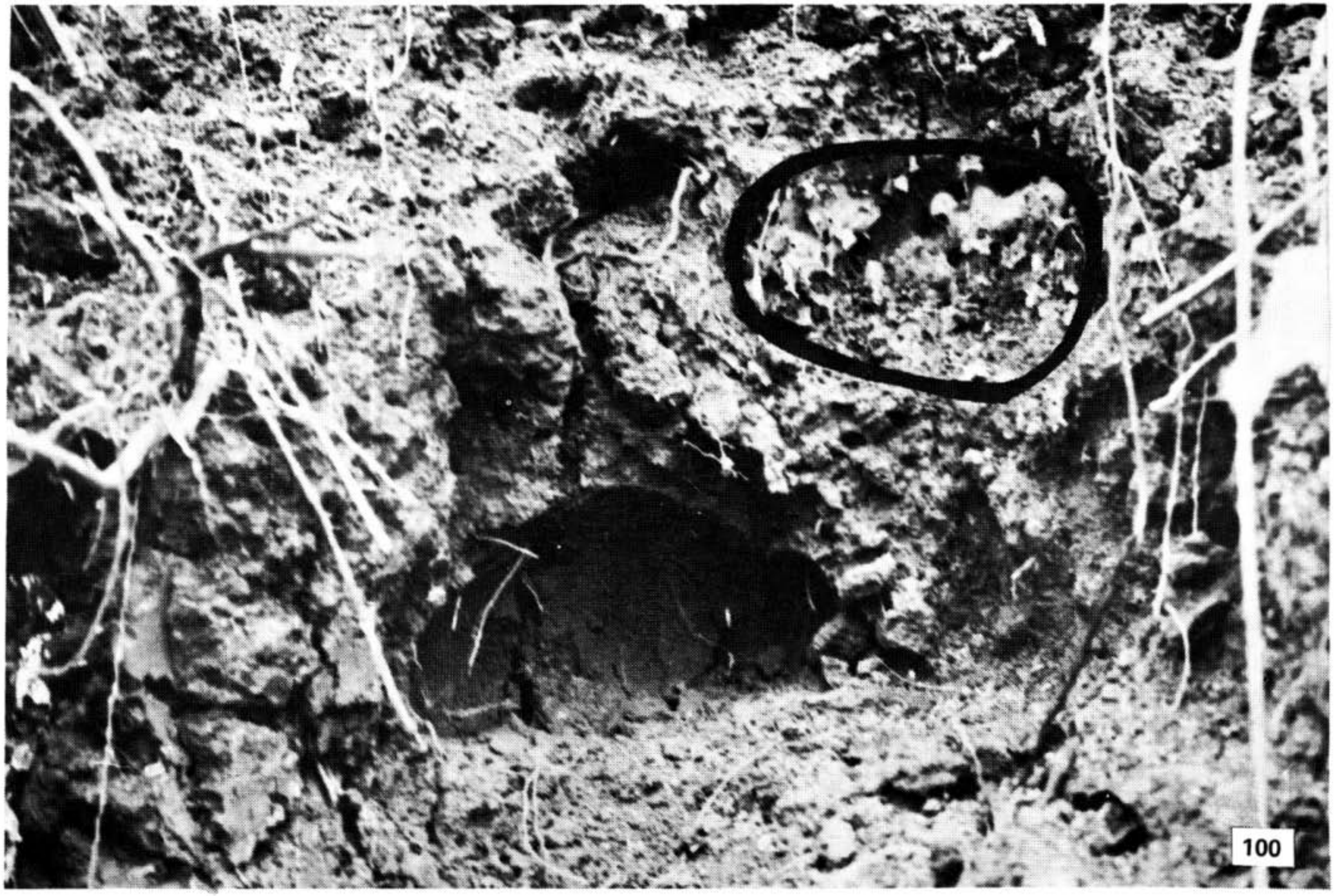
Figure 100. *T. (T.) j. jaty* (*sp.* 85), cavity where the nest was found, marked with a ring of black ink, the cavity partially filled with some pots and combs; there is another natural cavity below, similar to the one used by the bees.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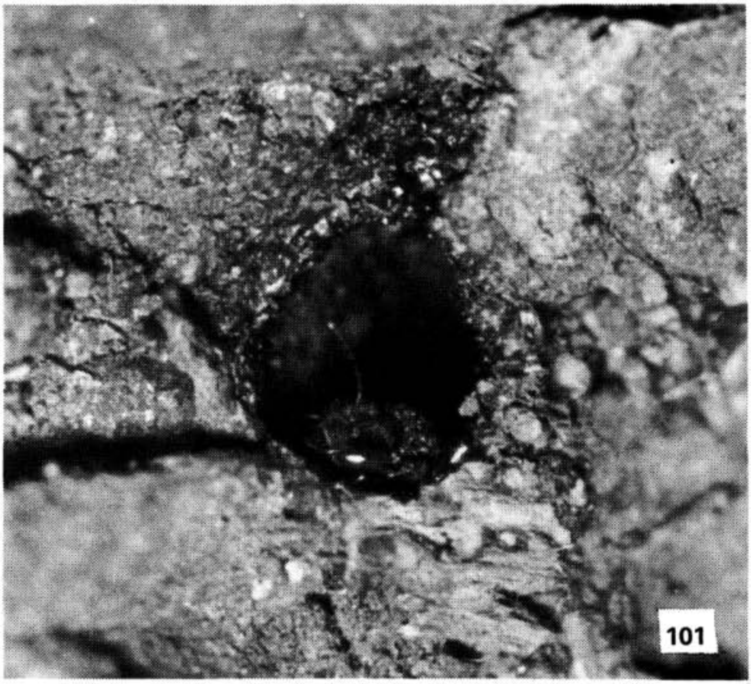
Figures 101, 101a. *Trigona (Tetragona) nigra paupera* (*sp.* 90), nest entrance.



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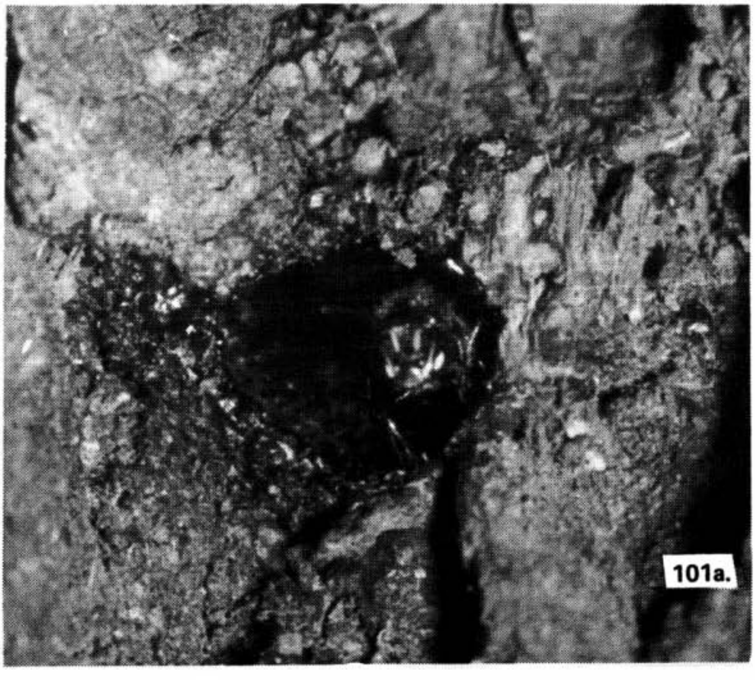
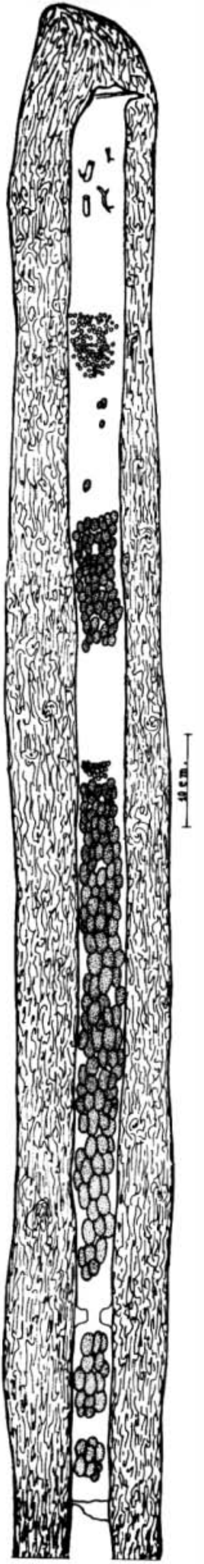


101a.

Figure 102. *T. (T.) n. paupera* (*sp.* 90), diagram of nest.



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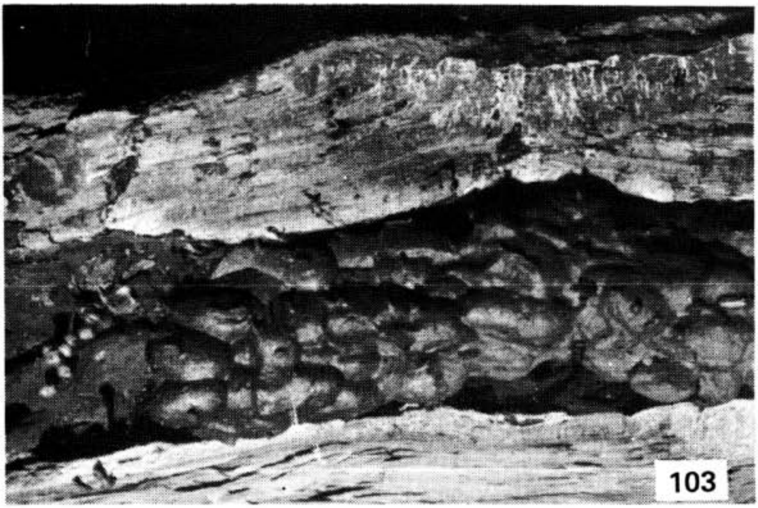
Figures 103 – 105. *T. (T.) n. paupera* (*sp.* 90), portions of nest in fence post.



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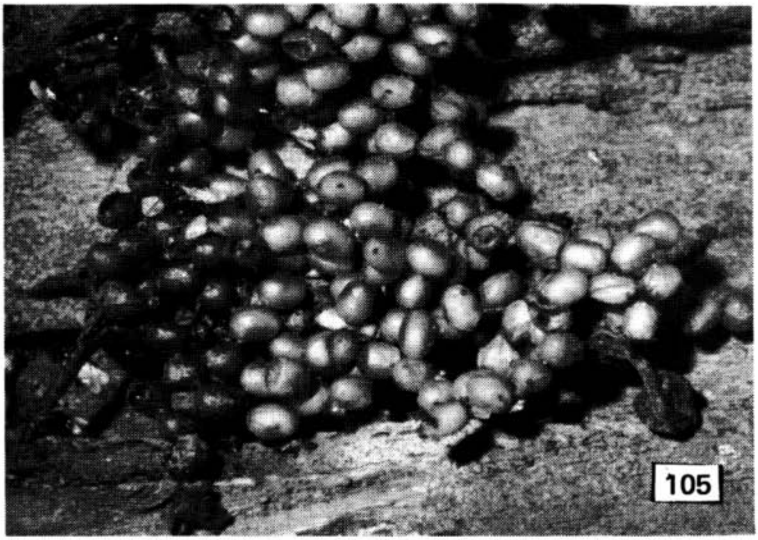

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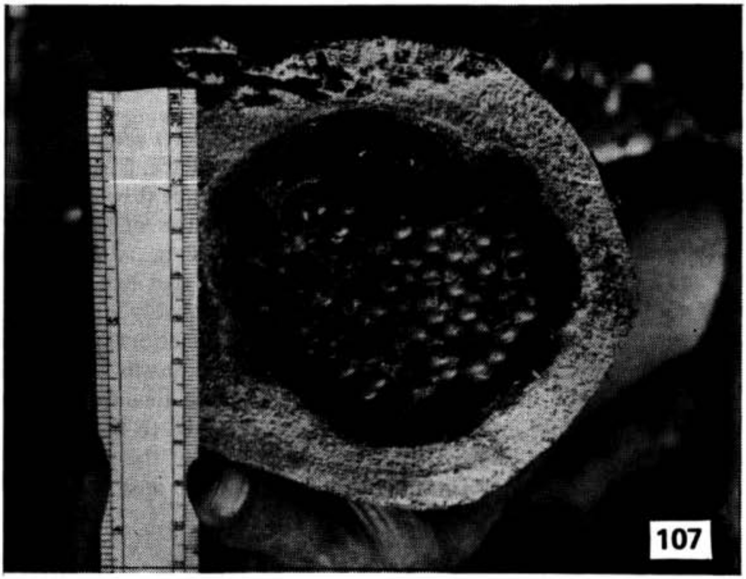
Figures 106–108. *T. (T.) n. paupera* (*sp.* 90), sections of nest in horizontal root. (photos taken by Ing. Luis Angel Salas).

106



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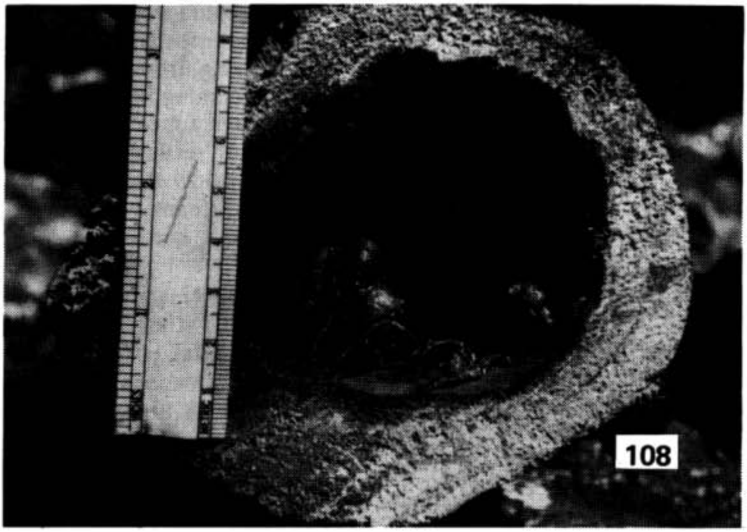

108

has been reported nesting in the ground, one of us (AW) found a nest in a road cut (figs. 97–100). Nest highly variable because of the variety of situations in which this species will nest. External entrance tube gray or brown, usually yellowish near apex, thin, pliable. Lining batumen and batumen plates black, plates rather thin and flexible. Involucrum light brown, of soft, thin sheets, 3–7 layers in different parts of the nest and up to 3 cm in total thickness; in nest in vertical tree hollows, involucrum is thin and of only 2–3 layers at sides, much thicker above and below. Food pots brown, walls thin, flexible; pots fused in groups but recognizable individually; pots above brood chamber in vertically oriented cavities, at side of brood chamber in horizontal box; honey pots mostly above pollen pots although some are intermixed; brood chamber variable in shape according to shape of cavity, number of combs correspondingly variable; failure in two nests to find any cells being built suggests synchrony in construction.

According to Leslie Johnson (personal communication) several colonies of *Trigona jaty* observed in February in Santa Rosa National Park, Guanacaste, Costa Rica applied to the outside of the typical soft yellow entrance tube a thick coating of sticky material which entraps ants. Stuck to the tube of one nest (figs. 93–96) there were 60 workers of *Camponotus silciventris,* an aggressive and omnivorous ant likely to collect *Trigona* brood and nectar if it had easy access; 5 *Acromyrmex octospina* and 1 *Pseudomyrmex,* the latter probably wanderers. Many ants were damaged, perhaps by the bees. The bees applied additional sticky material with their mandibles to ants that were still alive. The assassin bug *Apiomerus pictipes,* which preys upon other *Trigona* in the Santa Rosa area, would be unable to catch these *T. jaty* by its usual method, which is to crawl to the tube opening and snatch bees in transit. In early April, however, some of the same nests were noted by O. R. Taylor to have normal entrance tubes and no ants were seen in the vicinity.

90. *Trigona nigra paupera* (figs. 101 – 108). Entrance with only weak blackish rim of cerumen. Above bottom of one nest is batumen plate in which large hole has been opened, presumably for nest expansion. Lining batumen and batumen plates present, black, the latter irregular at times, one varying from 2 to 17 mm in thickness in different areas. Food pots dark brown, becoming light gray with age, the major cluster of them largely filling cavity in nest diagrammed; pots individually recognizable although fused; pollen pots in upper part of vertical nest, honey pots below, the two meeting in the long cluster; pots larger below than above, but this differentiation does not correspond perfectly with the difference in content. Cells brown, just touching or with short pillars or connections between them so that there are abundant spaces among cells; new cells at tops of clusters — whether they ever start again at the bottom of a cluster or start a new cluster elsewhere in the nest is unknown. Cells mostly directed upward. Cocoons straw colored, most of them with axes vertical but some slanting and even horizontal, perhaps having been loosened when the bees removed cerumen from them. Cocoons and pots often supported on rather long pillars, especially when there is little crowding as in horizontal nest.

91. *Trigona (Tetragona) perangulata* (fig. 109). Entrance black, brittle,

funnel–shaped but scarcely projecting beyond level of surface of tree trunk, 70–80 mm in diameter from outer margin to outer margin but throat 20 mm in diameter. Entrance hole passing through slender cavity full of humus or soil above, plugged below by pale brown sticky material of unknown origin, but with large region full of sheets of hard, blackish involucrum–like material. Cavity of nest with black batumen plate near bottom, but two holes allow bees to get to additional nest area below. Pots dark brown, walls soft, flexible, about 1 mm thick, fused but distinctly recognizable from outside; above brood chamber are both honey and pollen pots, generally in separate groups; below are only honey pots; honey pots average larger than pollen pots (Table 5) although there is intergradation. Brood cells dark brown, cocoons light brown, no layers of cerumen in space above advancing front, queen cocoons at margins of combs.

101. *Trigona (Trigona) corvina* (figs. 110 – 120). The oval, vertically elongate, exposed nests vary in weight from 8 to 162 pounds. The lighter and younger nest are also smaller in size, 34 x 43 cm for a nest weighing 8 pounds and probably under two months old, 35 x 45 cm for a nest weighing 20 pounds; the heavier older nests range in size up to 50 x 85 cm and 55 x 70 cm. It seems, therefore, that these nests grow some in size and enormously in weight as they become older. The presence of a partial batumen layer, not going all the way around, on the outside of the upper part of one nest suggests the way in which the nests grow in size. Growth in weight of course involves brood, storage pots, and cerumen structures but the main factor is the enormous gray or yellowish waste and earthen deposit ("scutellum") with which almost all spaces between all but the outermost and the innermost batumen layers are eventually filled so that the layering of batumen becomes difficult to see. Deposition of the waste–earth mixture seems to start in the upper part of the nest as shown by **Wille** (73). In a nest of median age many of the spaces in the upper part were partly filled (fig. 120). In one nest earthen material filled most of the spaces in the top, was reduced at the sides, but some such material continued down so that only a circular area about 10 cm in diameter at the bottom lacked it. Finally, in the largest and heaviest nest, an earthen layer completely surrounded the rest of the nest, 24 cm thick at the top, 9–11 cm thick on the sides and bottom. Access to spaces among outermost batumen layers of old nests seems to be through small passages in the earthen material near the entrance and in the upper part of the nest. The full development of earthen material must reduce space available for food pots and perhaps even the brood chamber, while at the same time providing for excellent protection and improved temperature control. In any event, the largest nests had relatively small colonies of bees, a fact also noted for this species and the related *T. spinipes* by other authors (39, 63).

Outer batumen dark gray, often weathering to pale gray, brittle, about 1.5–2 mm thick; next few layers also brittle in young nests, in older nests stronger; batumen layers 5–6 on sides and bottom of nest to 10 or more at top, maximum number not counted in largest nests where layering is obscured by earthen material but at sides reaching 12, at top probably considerably higher, layers 15–20 mm apart or only about 10 mm apart at sides, separated by pillars; total thickness of batumen 7 cm at bottom and sides and 16 at top in young nest to 13–19 cm at

Figure 109. *Trigona (Tetragona) perangulata (sp.* 91), diagram of nest.

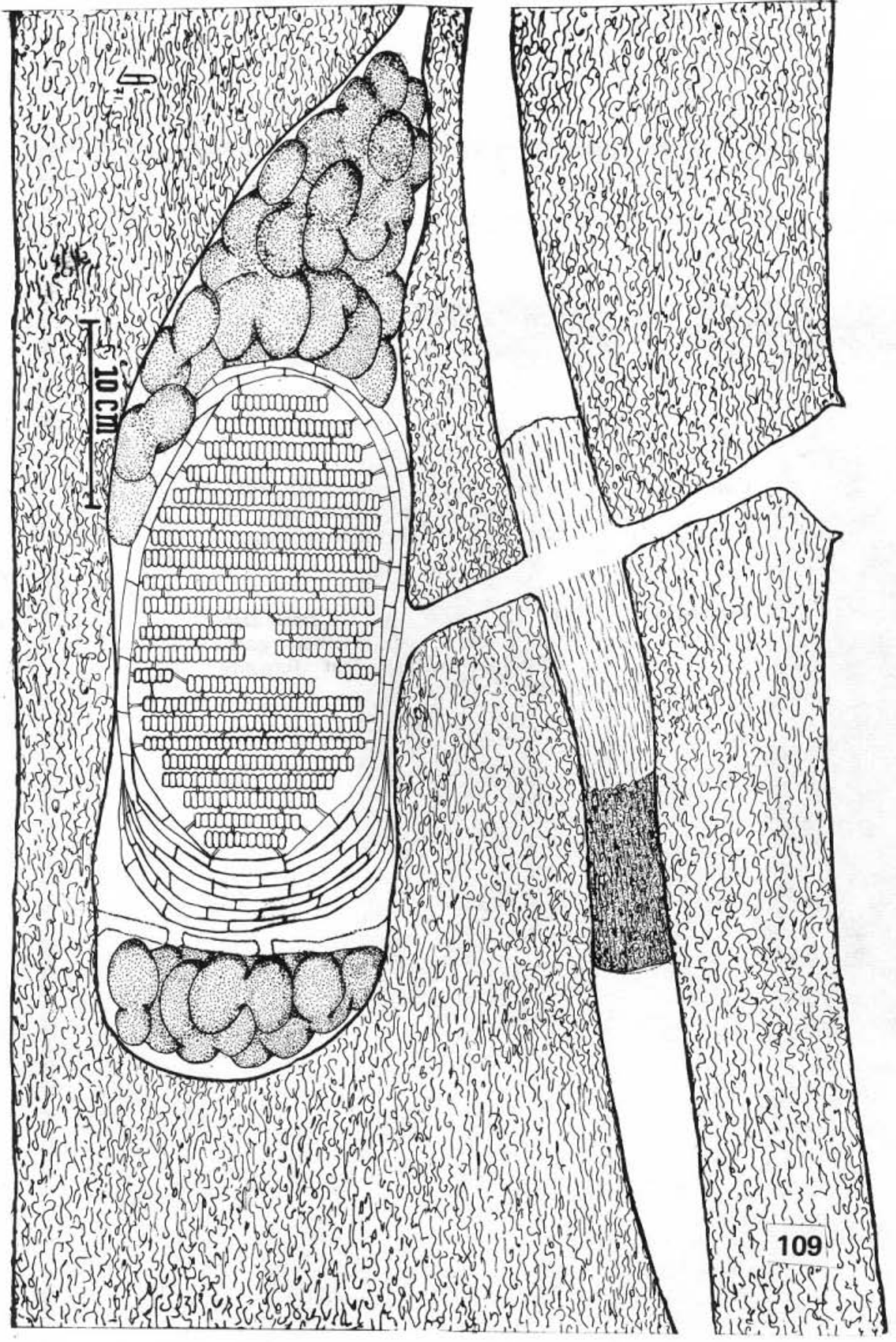

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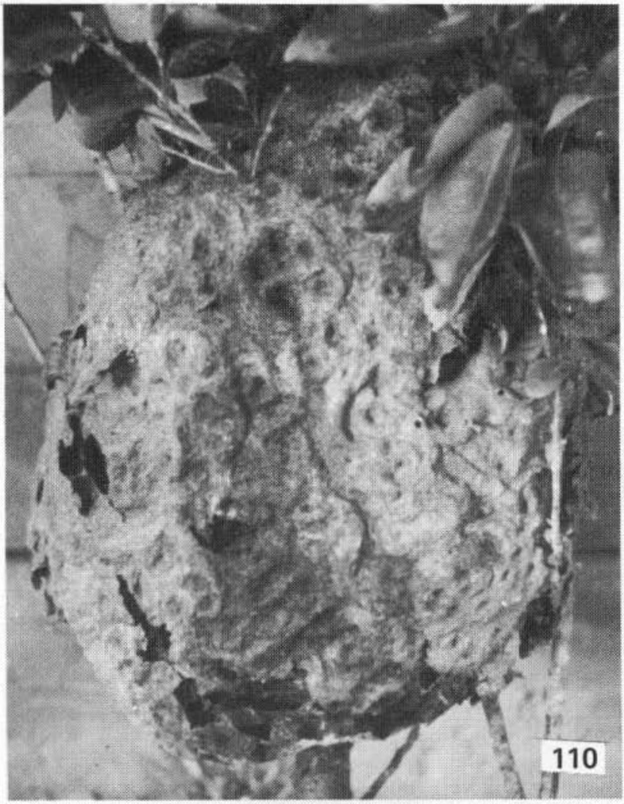
Figure 110. *Trigona (Trigona) corvina* (*sp.* 101), rather small nest, outer layer of batumen broken in various places.

Figure 111. *T. (T.) corvina* (*sp.* 101), small nest, outer layer of batumen gone, showing pillars that formerly supported it.



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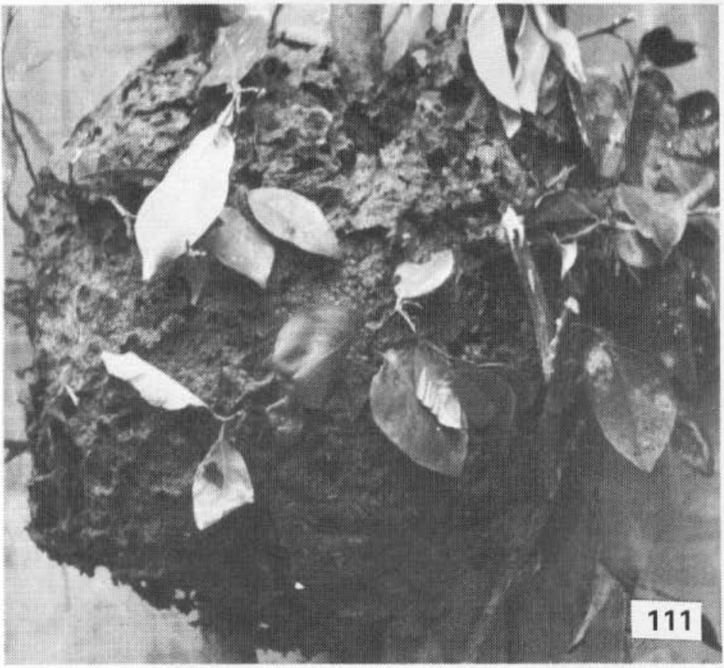
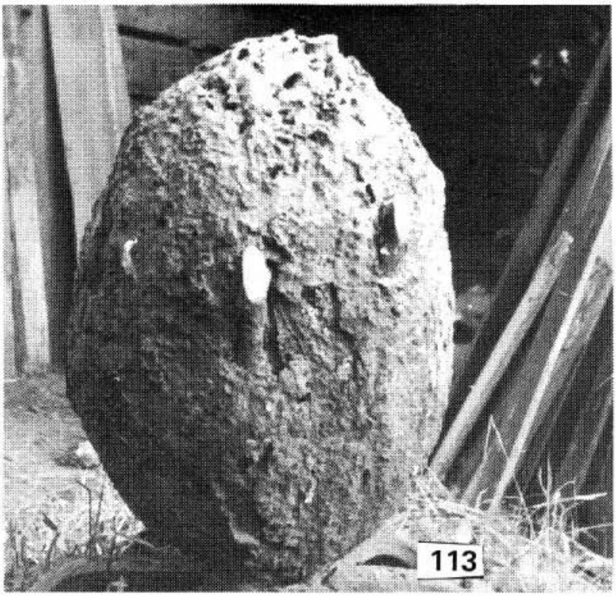


111

Figures 112–115. *T. (T.) corvina* (*sp.* 101), large nest removed from tree, earthen material removed from half of nest, and nest opened to expose brood combs.


112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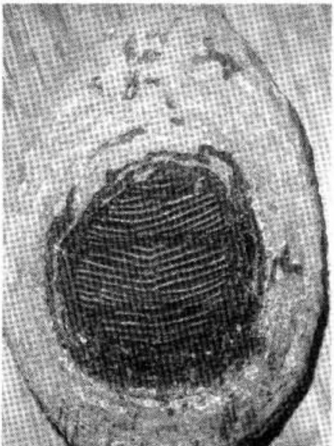
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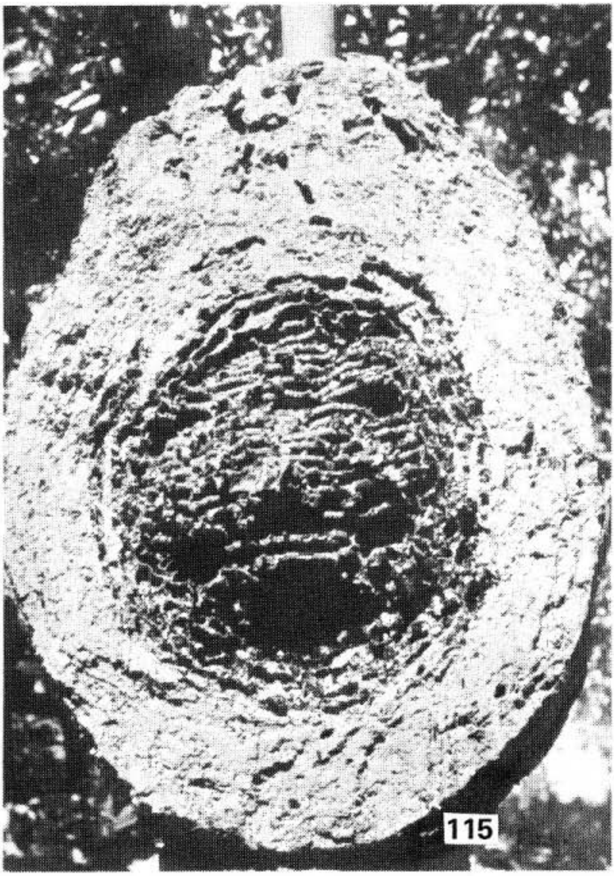
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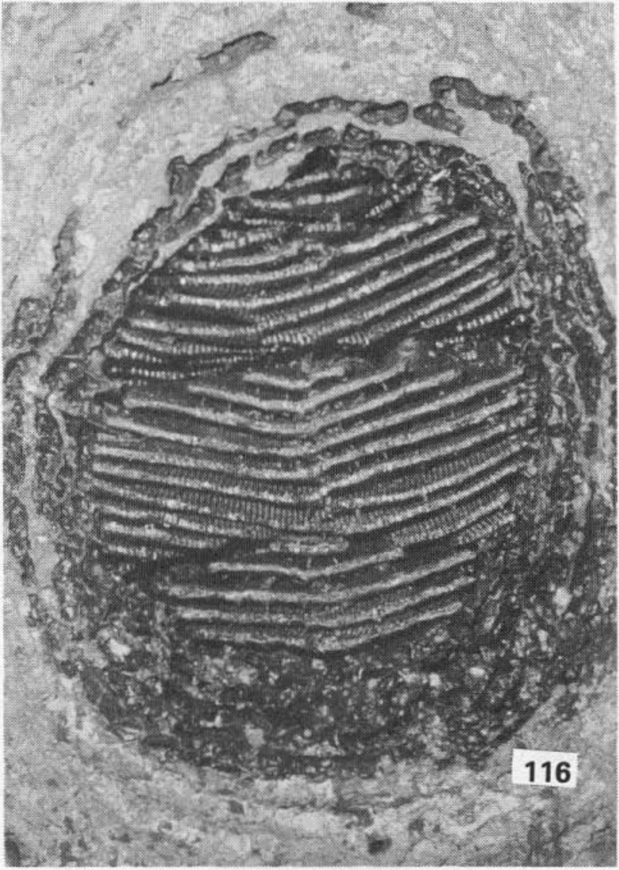
Figure 116. *T. (T.) corvina* (*sp.* 101), brood chamber showing three advancing fronts.

Figure 117. *T. (T.) corvina* (*sp.* 101), top view of a regular advancing front.



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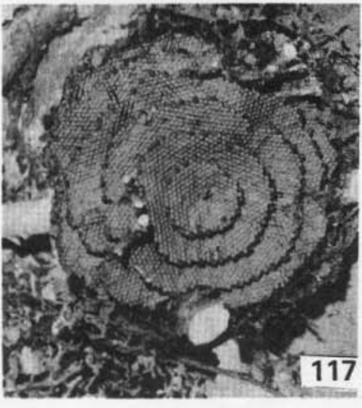
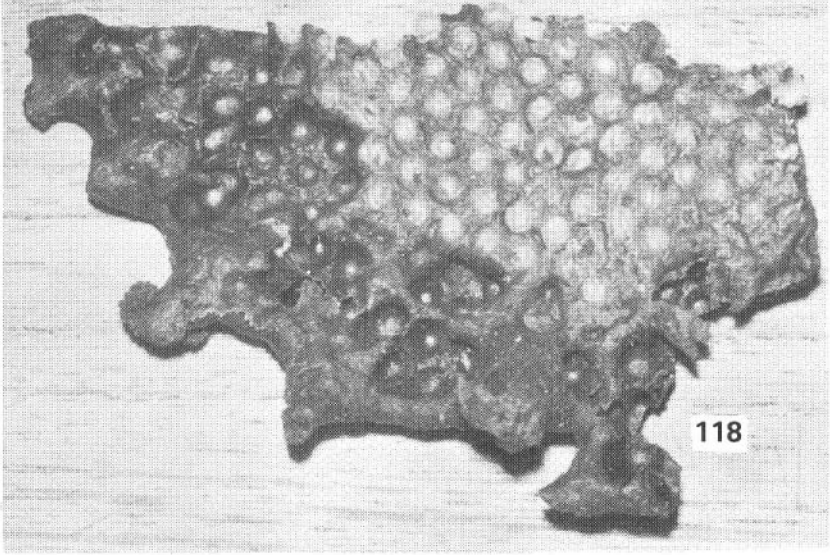


117

Figure 118. *T. (T.) corvina* (*sp.* 101), portion of atypical comb in which removal of wax from cocoons was incomplete, showing only their tops (upper right); on emergence of bees, cocoons are removed (lower left) leaving early stage of sheet with cocoon pattern on it.

Figure 119. *T. (T.) corvina* (*sp.* 101), longitudinally opened young nest.

Figure 120. *T. (T.) corvina* (*sp.* 101), section of upper part of nest of median age showing growth of earthen material.



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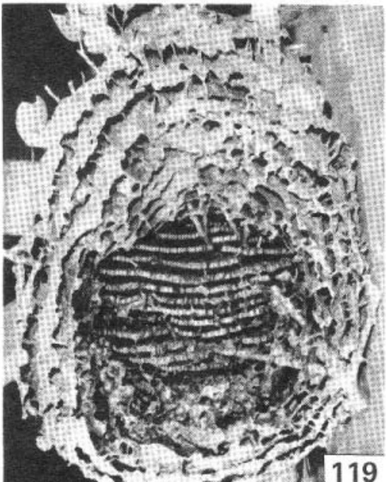

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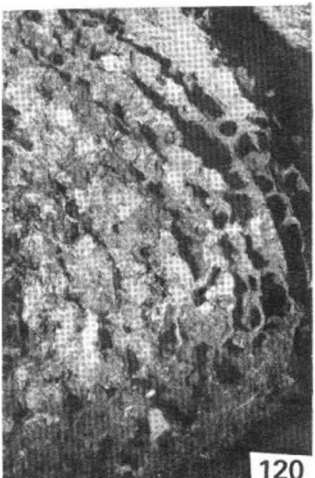

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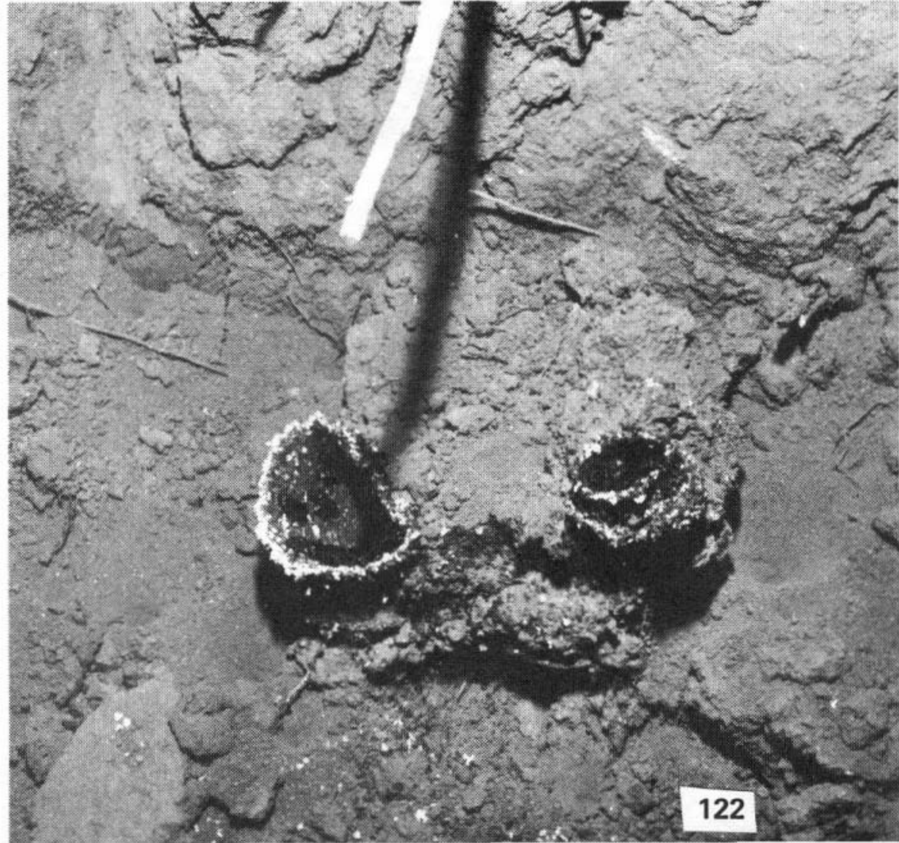
Figure 121 *Trigona (Trigona) fulviventris fulviventris (sp.* 105), nest entrance, usual form.

121

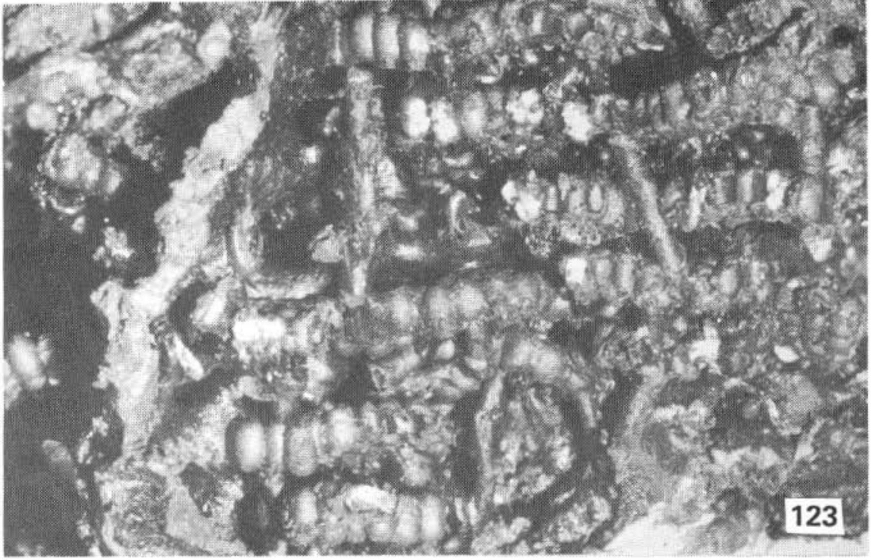
Figure 122 *Trigona (Trigona) fulviventris fulviventris (sp.* 105), nest entrance, double and not so dark.



122

Figure 123. *T. (T.) f. fulviventris* (*sp.* 105), portion of brood, showing near left a more or less vertical partition through brood chamber, and elsewhere, permanent pillars.

Figure 124. *T. (T.) f. fulviventris* (*sp.* 105), complete brood.



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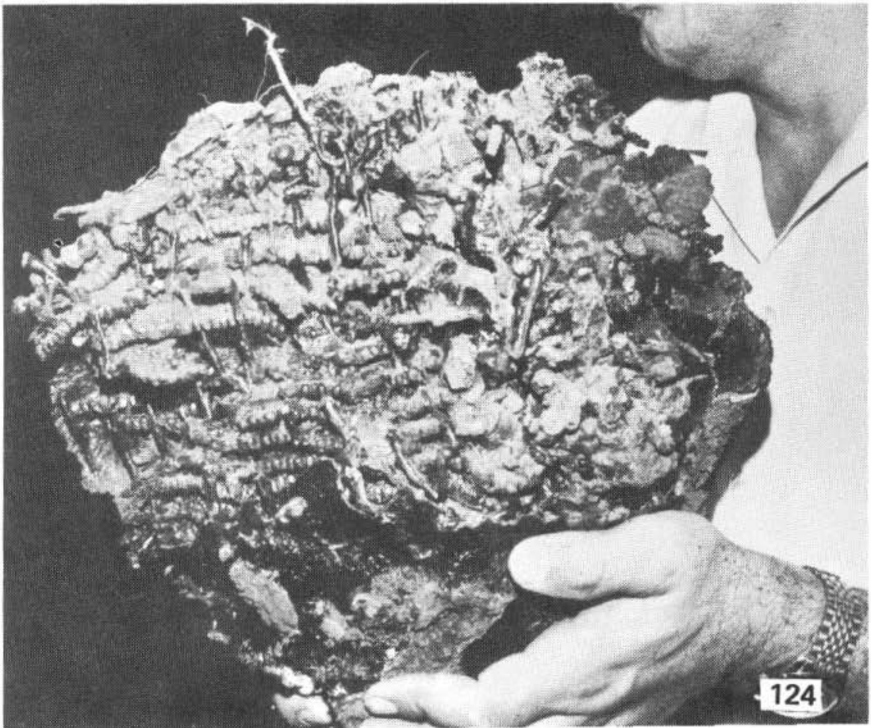

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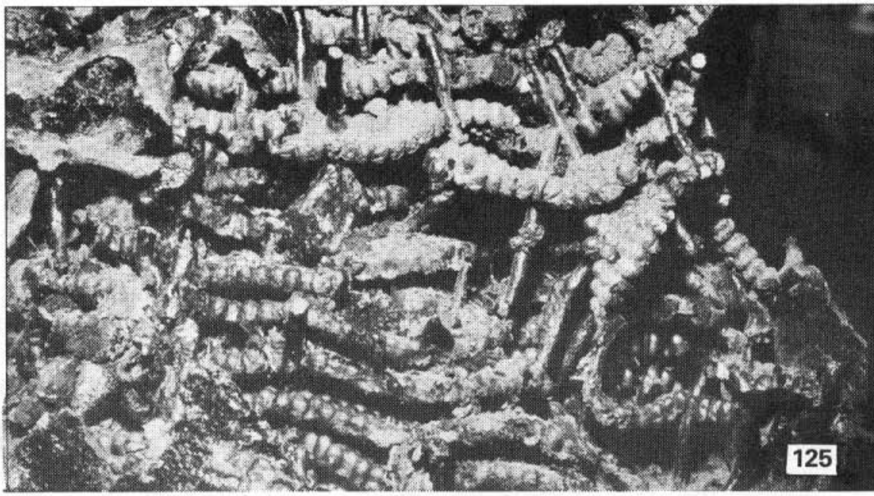
Figure 125. *T. (T.) f. fulviventris* (*sp.* 105), portion of brood, showing irregular combs and pillars.

Figures 126, 126a. *T. (T.) f. fulviventris* (*sp.* 105), food pots.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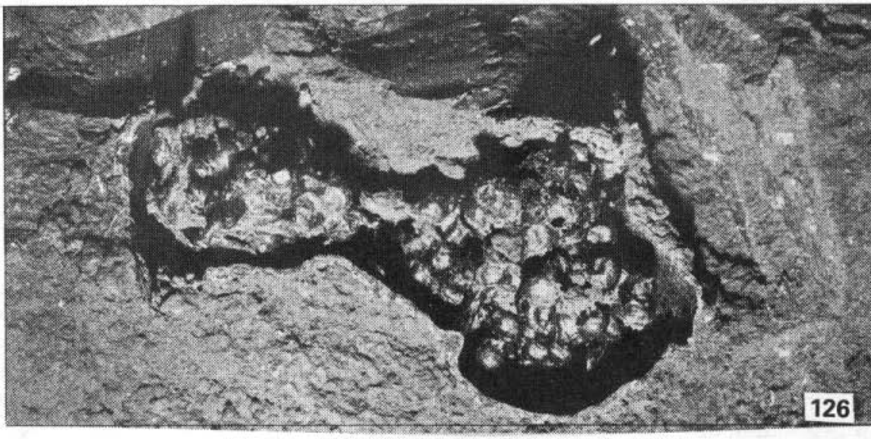
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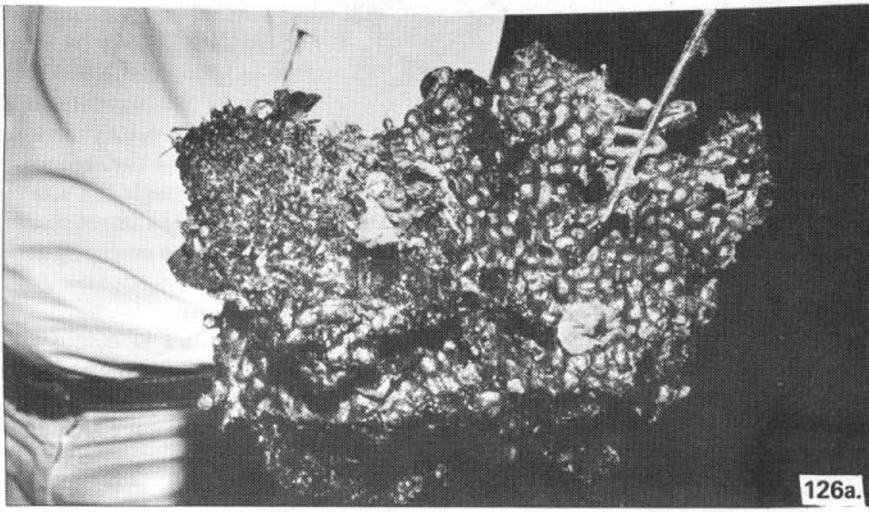

126a.

sides and 31 cm at the top in old nests; outer sheets at least in young nest with plant fibers evidently from cow manure incorporated. Pots light to dark brown (in different nests), between the inner batumen layers, principally in the lower part of the nest. Pots isolated or fused in small groups, individually distinguishable. Innermost enveloping sheet is internal to all pots and is soft and flexible, here considered an involucrum. No concentration of pots between involucrum and innermost batumen layer, but only the same number as between certain of the batumen layers.

Combs often very irregular, especially when branches and twigs of trees pass through them; combs partly spiral, partly not, even in same nest, never neatly uniform but with at least slanting connections and often with very irregular shapes; disassociated pieces of comb common; usually 2–3 advancing fronts at different levels in each nest, involving as many as seven combs in total, 2 or 3 at each front; in one large old nest with small population and only 10 combs, however, there was only one front and only two combs were involved; at any one front combs may be nicely regular (fig. 117). Cells dark brown; cocoons light brown. No sheets of cerumen constructed in spaces above advancing fronts.

In two old nests with small populations of adults, cocoons were only cleaned of cerumen at the tops, or not at all. On emergence of the bees, the cocoons were then removed but the cerumen on the bases of cells remained, leaving a membrane of cerumen with the cell pattern on it, as discussed above. An early stage in this process is shown in figure 118.

105. *Trigona (Trigona) fulviventris fulviventris* (figs. 121 – 126a). Exposed entrance of blackish, firm but flexible material, rough, the margin irregular (fig. 121), thickness up to 5 mm. Entrance tube through soil large, about 20 mm in diameter, lined by blackish material 1.5–2 mm thick, with light brown sticky material near entrance, perhaps for defense. Nest cavity lined with a blackish batumen layer; inside are various partitions and sheets of similar but harder material, mostly vertical, between which are pots; few horizontal black connectives up to 3 mm in diameter between sheets.

Pots dark brown, fused in small groups, individual pots often not recognizable from outside especially in case of honey pots. Brood area subdivided by various blackish sheets so that comb is irregular; no large combs covering entire brood area but only patches; no single brood chamber but a sheet of involucrum interrupted by partitions surrounds whole brood area; brood area also with rather numerous permanent vertical but somewhat irregular black pillars extending through several combs; no evidence of spiral tendencies in combs; combs start as single cell attached by side to pillar (as in *T. cupira)*; new combs started at all levels in various places in brood area; in each place where new cells were started, adults were emerging above, leaving space for new cells.

At least in this nest bees did not remove wax from cocoons.

Previous descriptions have not indicated such irregularities in combs as are described for the single nest described above, which, however, was large and active.

Wille (73) illustrates an entrance hole of this species in the ground with no projecting tube. Possibly it was at a nest being organized rather than the entrance of an established colony.

107. *Trigona (Trigona) fuscipennis* (figs. 127 – 133). Nests in cavities of *Nasutitermes* nests, bottom of one cavity with bird egg under bees' nest, showing that cavity was used and probably made by a bird. Entrance on outside of termite nest is funnel-shaped or ear-shaped, projecting 3 cm, up to 13 cm in diameter from margin to margin, throat 5 cm in diameter; entrance of brittle material. Cavity in termite nest lined with brown or black laminate batumen, mostly two to four layers, where crowded by convexity of cavity wall, only one layer. Food pots dark brown, fused in small clusters or isolated, mostly below brood chamber but a few at sides and above in one nest; pots of any one cluster usually all with honey or all with pollen. Many pots supported by pillars which extend up through brood chamber. Involucrum of one incomplete, soft, brown sheet, or absent, in the latter case pots sometimes attached to edges of combs. Brood chamber with various permanent vertical pillars, irregular, 3–4 mm in diameter, flattened to 10 mm wide, sometimes branching, hanging from top of nest and extending down among pots. Around or beside pillars are openings in combs 2–5 mm in diameter. Combs irregular, often patchy or of curious shapes, often forming irregular spirals around pillars, but independent new combs also arise where a spiral cannot conveniently be extended, to form a new layer.

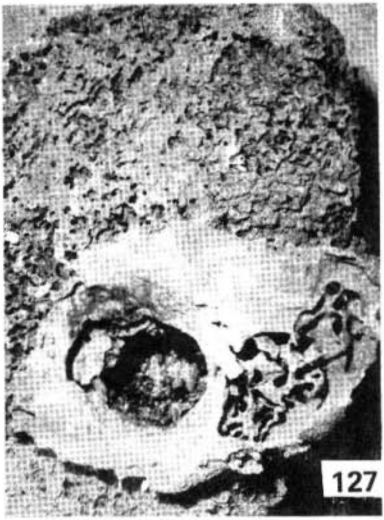
111. *Trigona (Trigona) nigerrima* (figs. 134–137). Large exposed nest, light compared to mature nests of *T. corvina,* our two estimated at 2 and 10 or 12 lb. The basic organization is as in *T. corvina* but the earthen material was not abundant in either nest found and its deposition was among batumen layers at the bottom of the nest rather than at the top. In both nests the batumen was about the same thickness all around the nest, 9 cm, not thicker above as in *corvina.*

Entrance rigid, dark gray, brittle, its wall 1–2 mm thick. Outer layer of batumen about 0.5 mm thick, irregularly bumpy, flexible, delicate, made almost exclusively of dung (apparently cow, pig, and dog); odor and texture do not show presence of added resin or cerumen but such material probably present to prevent weathering; nest surface partly greenish with algae, moss, and lichens which would help to prevent damage by rain; outer layer easily broken off, about 15 mm from next layer, the two separated by numerous pillars; other batumen layers blackish, harder, more brittle, 6–7 in number, 0.5–4 mm thick and 4–10 mm apart. Pots brown, in a mass below brood chamber, largely fused but very clearly recognizable, not scattered between batumen layers as in *T. corvina,* honey pots mostly below pollen pots in one nest but mixed in the other. One to four sheets of involucrum separate pots from brood chamber, outer sheets like batumen sheets, inner ones soft and brown; one partial soft sheet continues around sides and top of brood chamber in one nest. Brood cells dark brown, cerumen so thick that individual cells are hard to recognize at margins of combs; cocoons light brown. Combs much more regular than in other *Trigona (Trigona)* described here, although margins of some with broad irregular lobes; only one advancing front consisting of 2–4 combs; no permanent pillars; queen cells mostly on margins of combs.

114. *Trigona (Trigona) silvestriana* (figs. 138 – 140). Nests largely exposed but resting on large limbs or between bases of palm leaves, not around small

Figures 127, 127a. *Trigona (Trigona) fuscipennis* (sp. 107), nest entrance (broken and showing pillars inside of lobe) on nest of *Nasutitermes*.

Figures 128–130. *Trigona (Trigona) fuscipennis* (sp. 107), views of combs showing irregularity, vertical pillars, and food pots below; fig. 130 showing irregularity as seen from above.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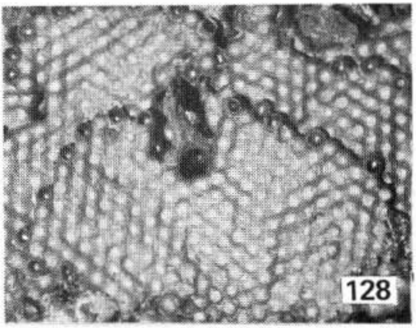
127a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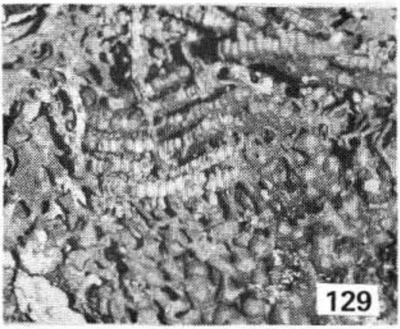
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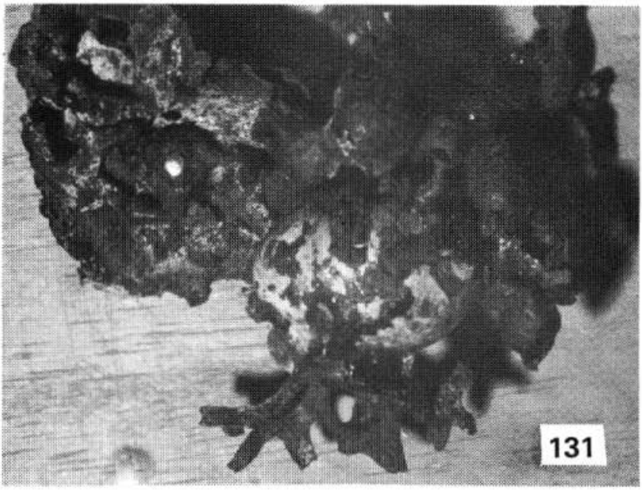
130

Figure 131. *T. (T.) fuscipennis* (*sp.* 107), birds egg at bottom of nest.

Figures 132, 132a. *T. (T.) fuscipennis* (*sp.* 107), vertical section through nests.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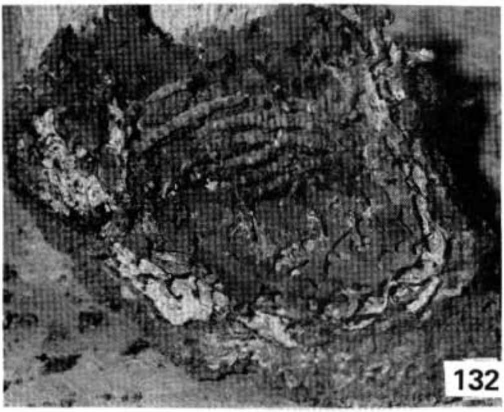
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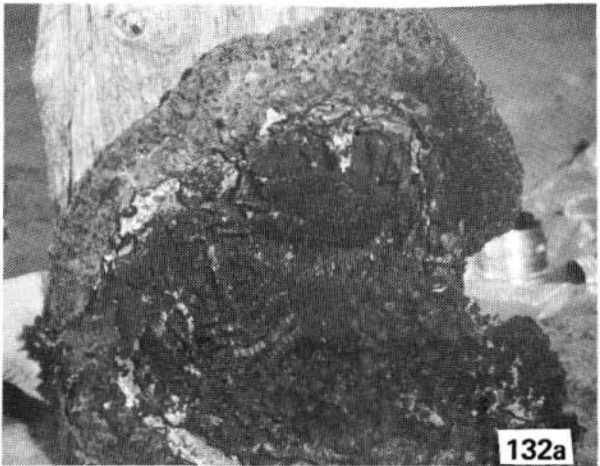
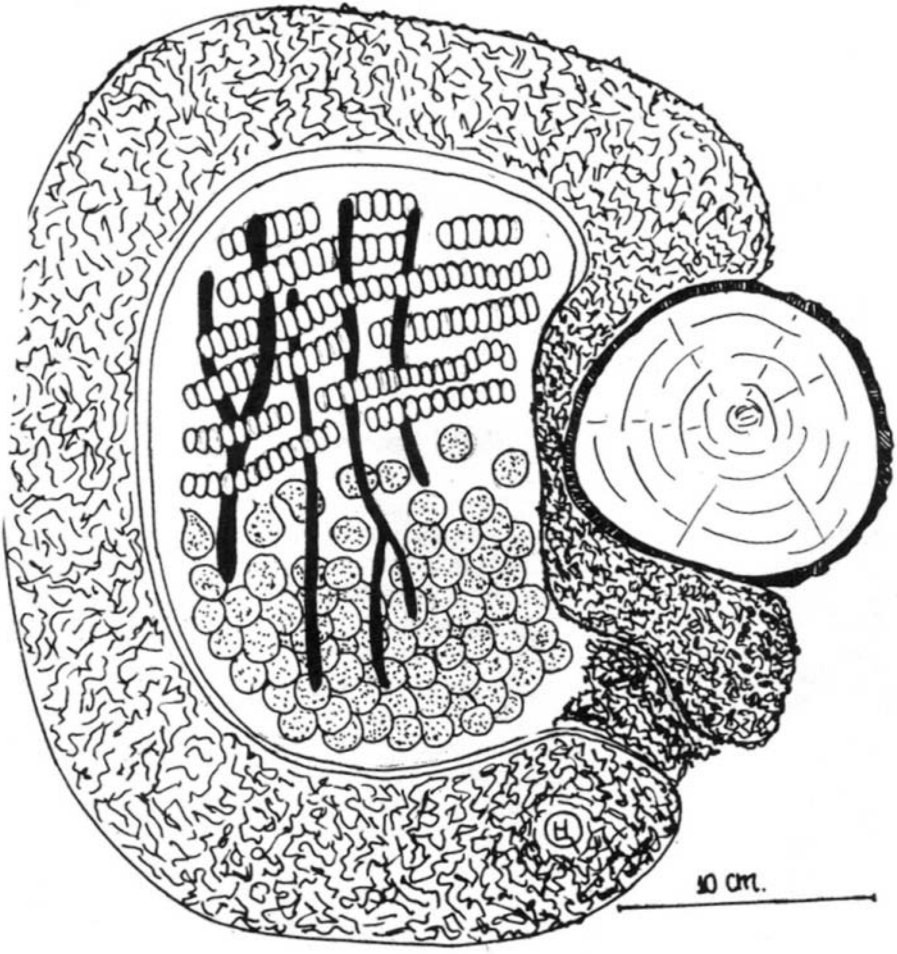

132a

Figure 133. *T. (T.) fuscipennis (sp.* 107), diagram of nest organization vertical section through nest in a termite nest.



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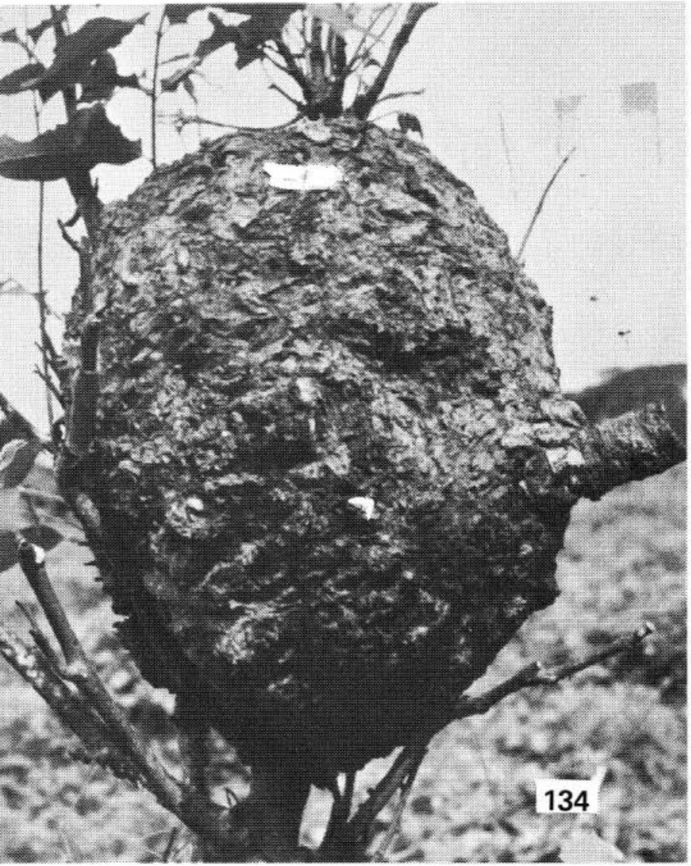
Figures 134, 134a. *Trigona (Trigona) nigerrima* (*sp.* 111), intact nest.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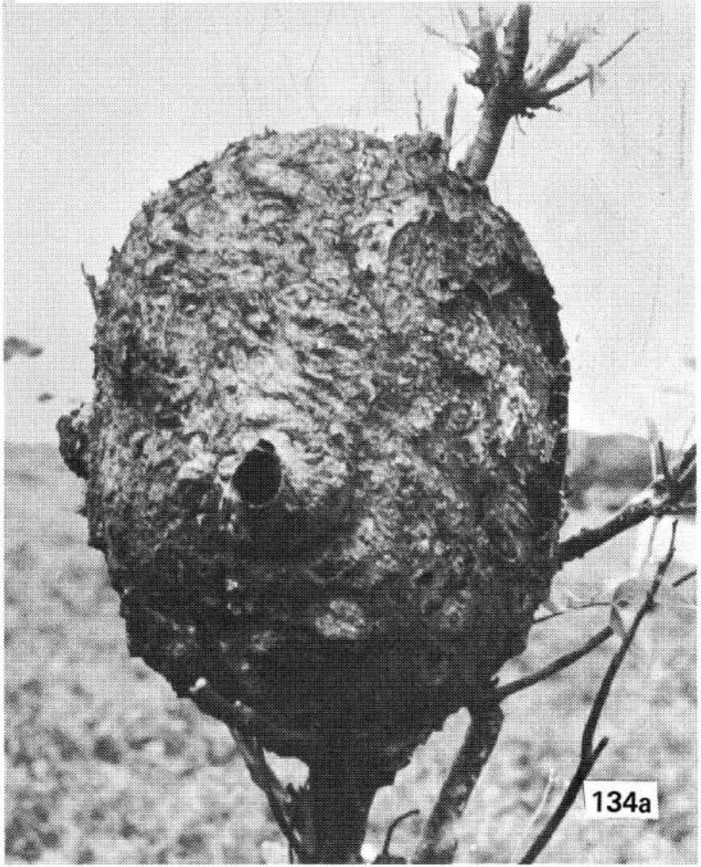
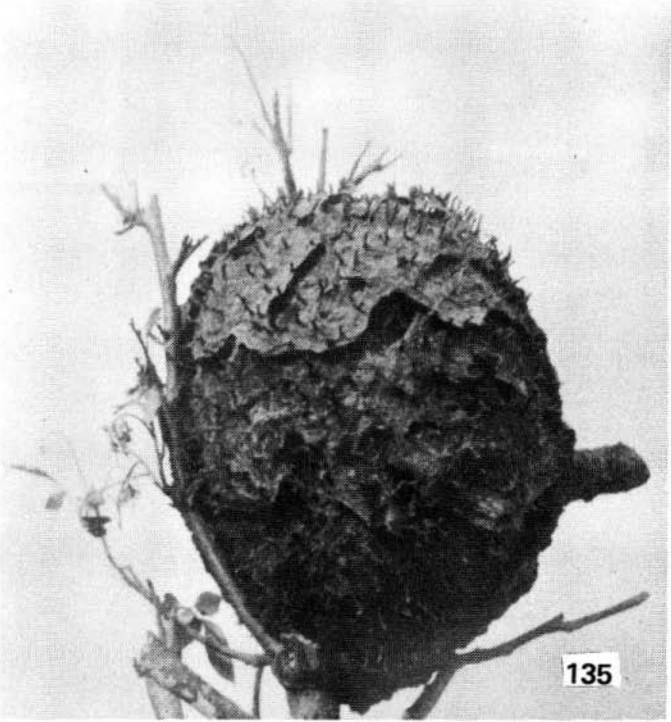

134a

Figure 135. *T. (T.) nigerrima* (*sp.* 111), nest with outer, brittle batumen layer gone, showing the numerous pillars that supported it.

Figure 136. *T. (T.) nigerrima* (*sp.* 111), opened nest, outer batumen layer gone.



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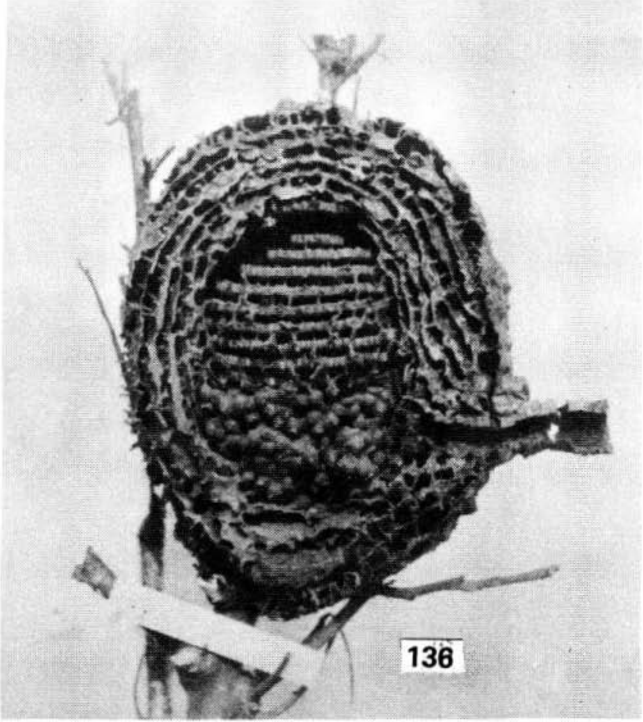

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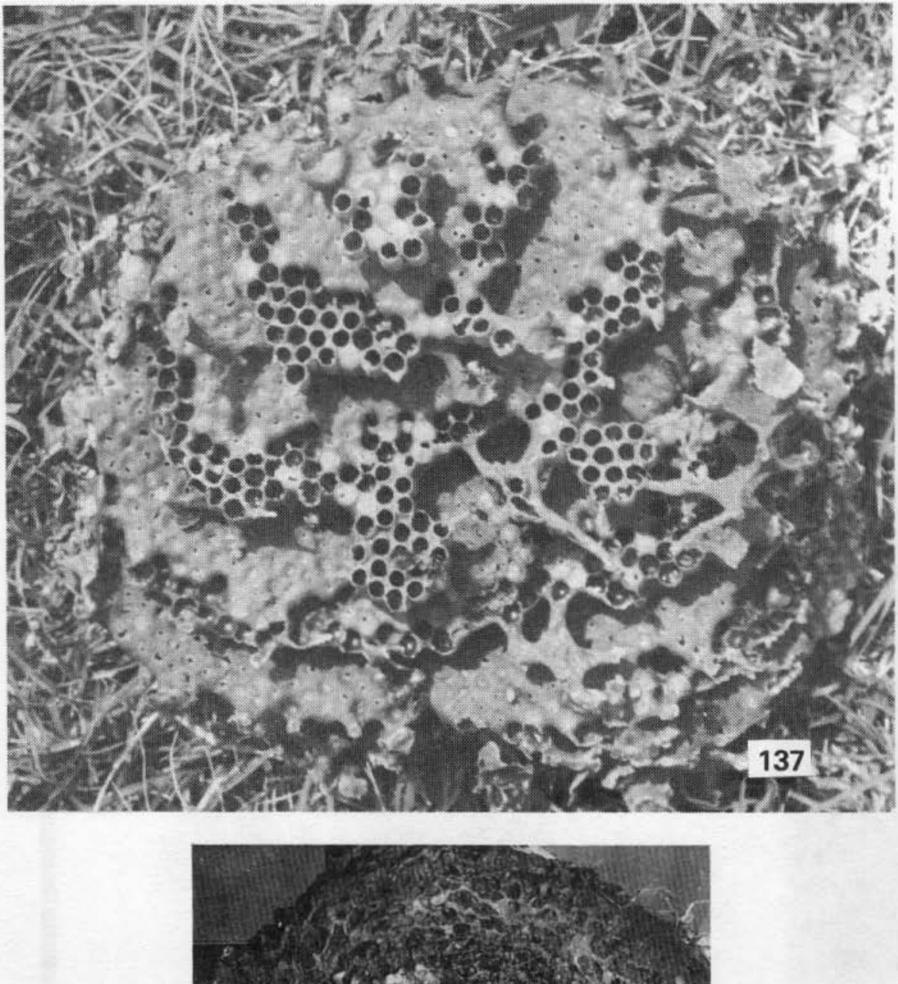
Figure 137. *T. (T.) nigerrima* (*sp.* 111), combs viewed from above, showing irregular shapes; most of cells perforated or opened.

Figure 138. *Trigona (Trigona) silvestriana* (*sp.* 114), vertical section through nest.



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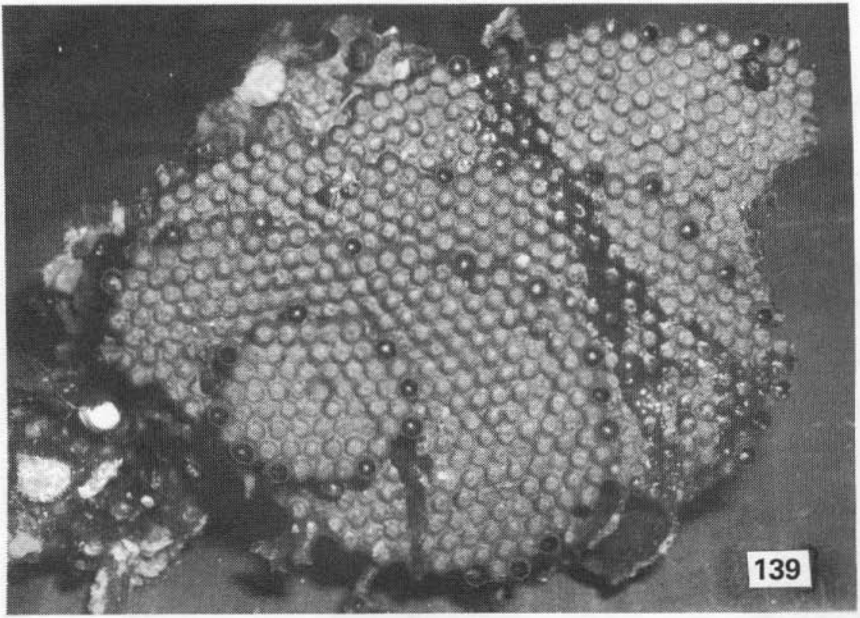
Figures 139, 140. *T. (T.) silvestriana* (*sp.* 114), top and side views of combs.



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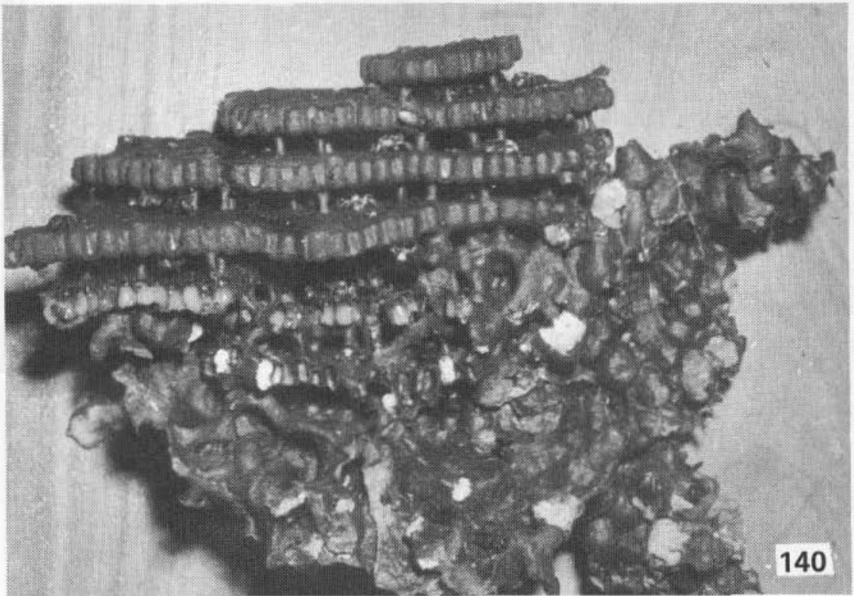

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Figures 141, 142. *Lestrimelitta (Lestrimelitta) limao* (*sp.* 119), diagrams of nest and nest entrance.

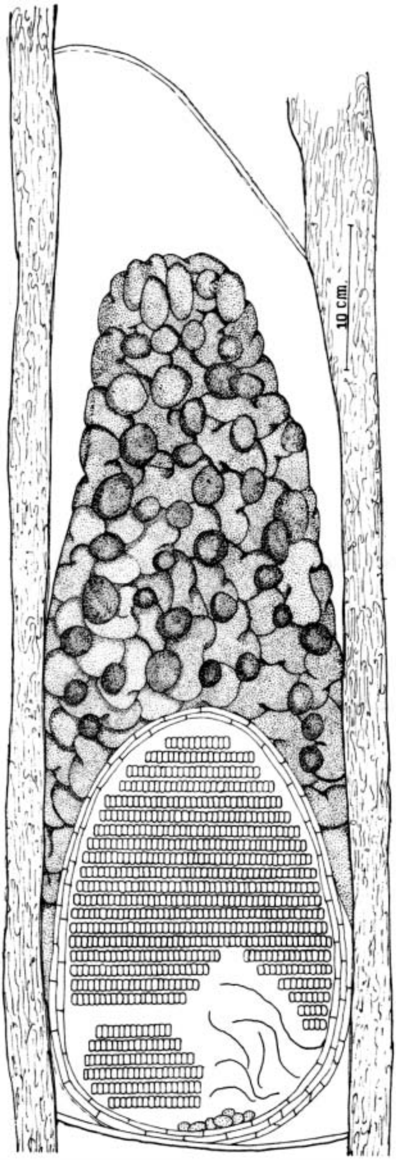

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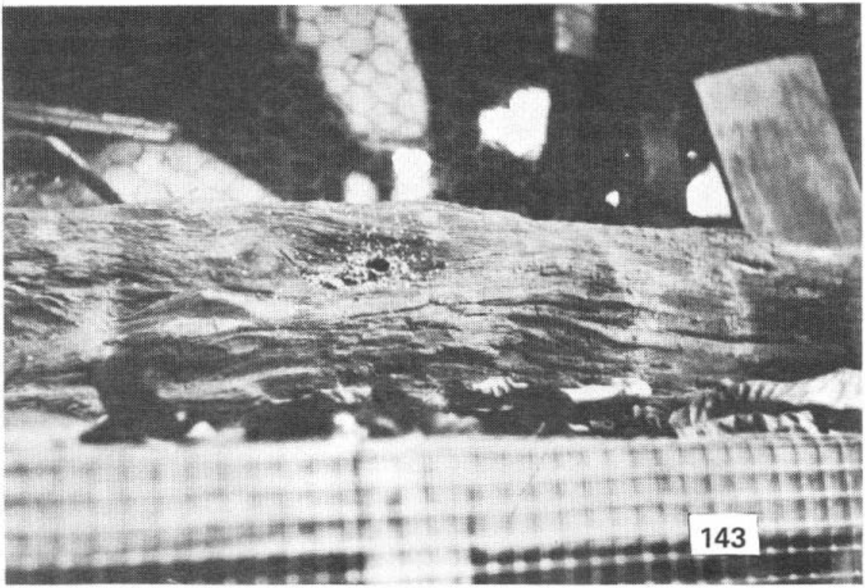
Figure 143. *Melipona beecheii* (*sp.* 122), nest entrance.

Figure 144. *Melipona fasciata fasciata* (*sp.* 124), nest entrance.



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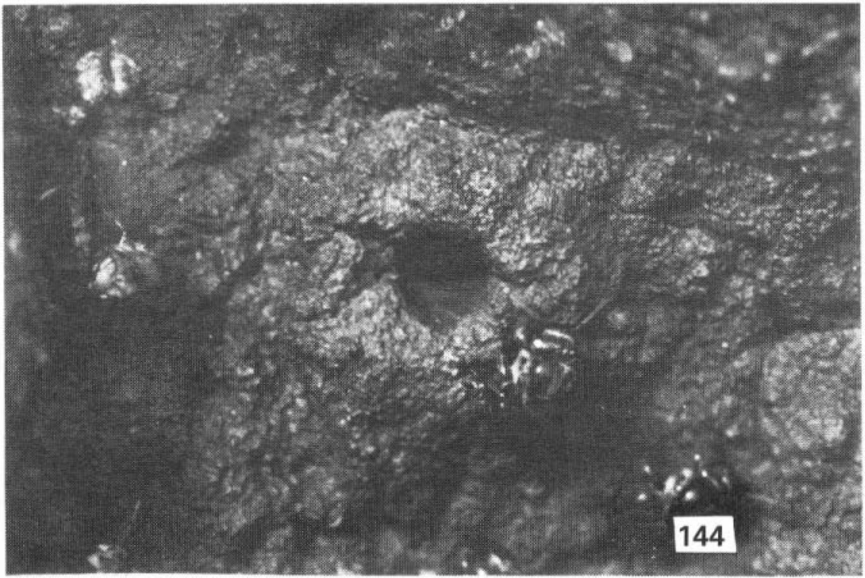

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Figure 145. *M. f. fasciata (sp.* 124), nest entrance.


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Figure 146. *M. f. fasciata* (*sp.* 124), diagram of nest.

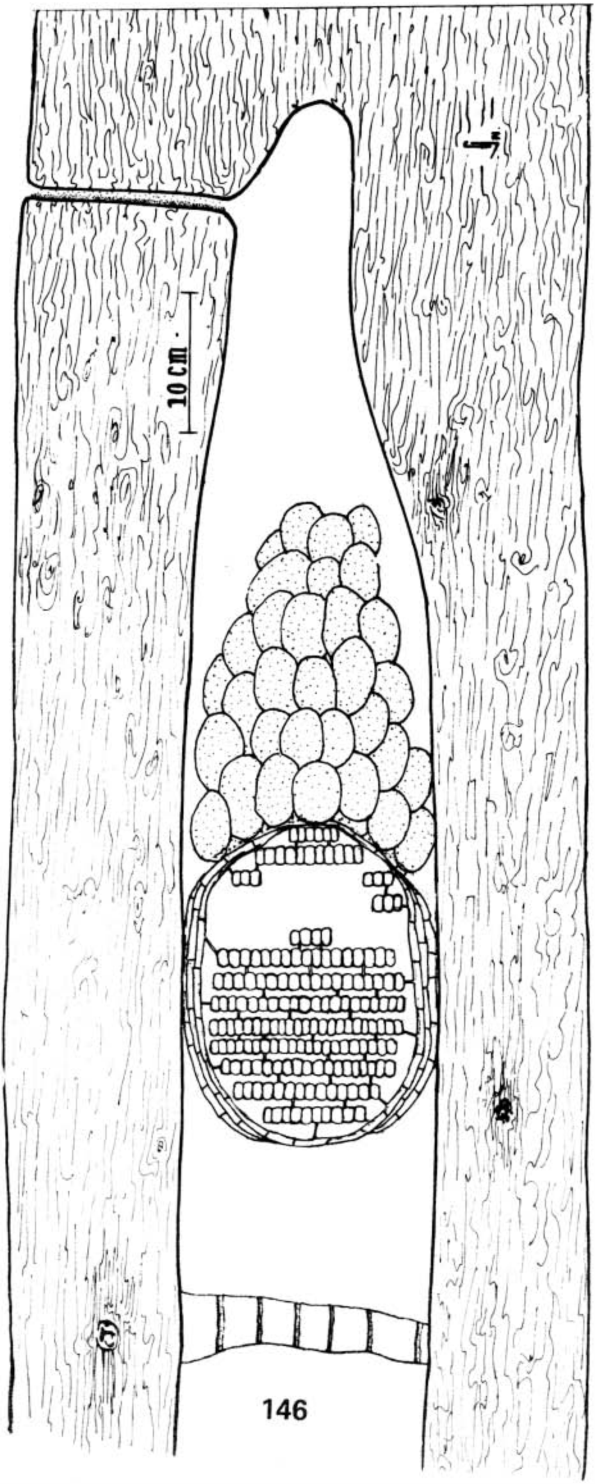

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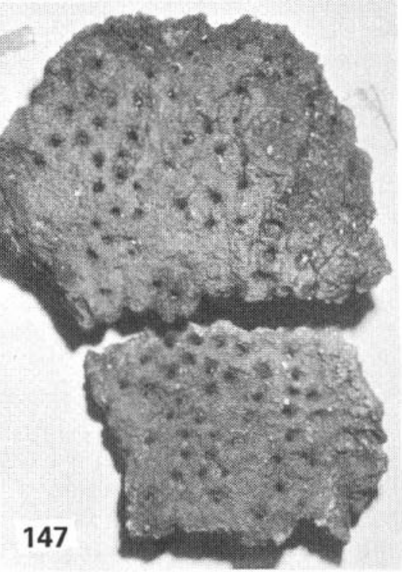
Figure 147. *M. f. fasciata* (*sp.* 124), batumen plate.

Figure 148. *M. f. fasciata* (*sp.* 124), storage pots.

Figures 149, 150. *M. f. fasciata* (*sp.* 124), comb, with pots above it in fig. 150.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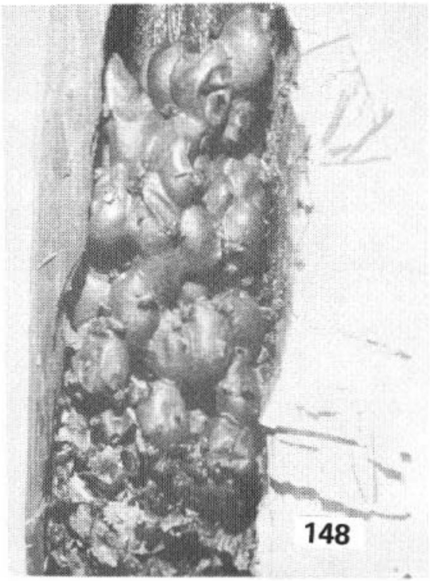
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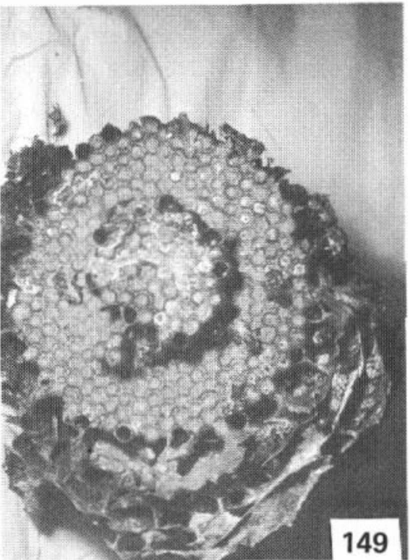
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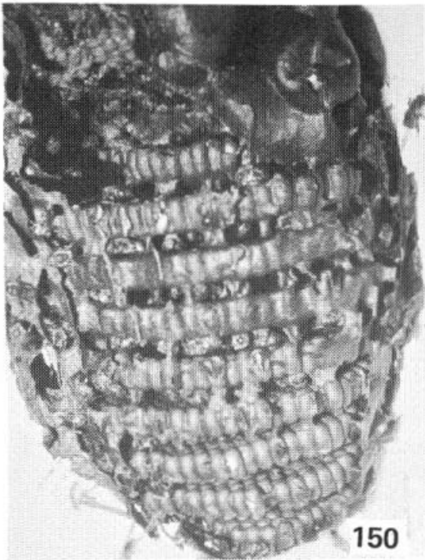
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branches like those of *T. corvina.* Entrance slightly funnel–shaped, width at apex 10 cm but throat 5 x 6 or 3 x 7.5 cm, walls 8–12 mm thick, of hard blackish material, leading into area of pillars and connectives in one nest, in other nest divided into two openings in throat. Batumen layers about seven with total thickness 10–18 cm where nest is exposed, but where nest is against substrate reduced to three layers or even a mere lining batumen; outer layer of batumen 1–3 mm thick, gray, includes much manure; other layers strong, blackish, 2–5 mm thick, or in places as much as 15 mm thick, in some places very irregular. Pollen pots between the inner batumen layers as in *T. corvina.* Involucrum absent in one nest, represented by small, scattered, irregular patches between brood and pots in the other. Brood chamber without permanent pillars but in one nest partially divided by vertical walls of cerumen into three parts. Combs irregular even in nest with undivided brood chamber, 10–11 layers in one nest, about 20 in the other, a given layer sometimes slanting up at one point to the next; spiraling evident in some places, not others. Thus in one nest eight combs below an advancing front were separate, ten combs above were spiraled, but two above that were separate; in other nest there was no spiraling; two advancing fronts in nest with undivided brood chamber, one for each group of combs in other nest. Earthen material was present among batumen layers in a nest described by **Myers** (37).

119. *Lestrimelitta limao* (figs. 141 – 142). Entrance tube black, of hard material about 7 mm thick, with thick hollow protrusions hanging down at base and sometimes on lower surface; no entrances found with slender root–like projections like those in southern South America; inside entrance a complex of anastomosing pillars and connectives which also extends into most of the projections. Cavity with two black batumen plates and thin lining batumen. Storage pots blackish, above brood chamber, fused and with much cerumen on outside so that lines separating individual pots are not clear from outside. Involucrum of two or in places three layers, connected by short pillars, outer sheet hard and black, inner one soft and brown. Brood chamber with one advancing front, empty space at lower right (fig. 141) filled with sheets and pillars of cerumen. Cells dark brown, cocoons pale brown.

122. *Melipona beecheii beecheii* (figs. 143). Entrance merely a hole with a slightly raised rim and some mud around it; no distinctive pattern. Nest cavity closed by the usual perforated batumen plates, in one of which was located the entrance. Storage pots at the two sides of the brood chamber (cavity in horizontal branch and therefore horizontally elongated). Involucrum of 1–4 layers, in most areas 2–3, mostly soft. Brood chamber with two sets of combs side by side, probably because it is horizontally rather than vertically elongate, one set with four combs, the other with eight.

124. *Melipona fasciata fasciata* (figs. 144–150). Entrance an unornamented hole with mud around it, in one nest in a perforated batumen plate 5 x 7 cm which closed the cavity in which nest was located. Cavity with thin black lining batumen and one or two batumen plates, 4–6 cm thick, perforated with holes up to 2.5 mm

in diameter at outside but about 1 mm in diameter through the plate, plates seem to be of mud with resin or propolis added. Storage pots with some to much fusion but very clearly separated, dark brown, black when old, walls only 0.5 mm thick, flexible; honey pots mostly above pollen pots. Involucrum of two to four dark sheets or at top between brood chamber and storage pots, of only one broken layer. Cells dark brown, cocoons brown; advancing front on two combs; nest in fallen trunk adjusted to new position by having two groups of combs side by side in one horizontal brood chamber, one group of three combs, the other of five, with advancing front on only one comb; combs broadly attached to inner sheet of involucrum.

125. *Melipona fasciata melanopleura.* Entrance an unornamented hole in small mud plate closing knot hole. No differences between comments on *M.f. fasciata* and the nest of *melanopleura* except that the latter has involucrum of six layers below brood chamber, four above, and only one around sides. These are presumably only individual differences and suggest no subspecific characters.

128. *Melipona flavipennis* (figs. 151–153). Entrance pale, of cerumen, not mud. Batumen plate thin, looking more like a cerumen plate than a mud plate. Pots fused but very distinct individually. Involucrum of several layers.

133. *Melipona marginata carrikeri* (fig. 154–155). Entrance not ornamented. Batumen plate of the usual *Melipona* type, with perforations. Comb neatly spiral.

The presence of an involucrum and the spiral comb, which is unique in the genus, suggest that *carrikeri* may be specifically distinct from the South American forms *amazonica* and *marginata* proper (Table 4).

ADDITIONAL INFORMATION ON COSTA RICAN MELIPONINI

Certain features of the Costa Rican bees, learned as a result of opening nests for study, seem worth recording at this time. One is the population. Table 6 gives data on colonies where we have reasonably accurate counts. We have the impression that colony size for some *Trigona* may have been exaggerated. It is true that very large nest populations rarely are counted because of the work involved. Yet the figures shown in Table 6 are notably low, as are published figures that seem to be based on counts or careful estimates, e.g.:

T. braunsi: 400–750 (**Bassindale, 1; Pooley & Michener,** 43)

T. araujoi: 2500 (**Michener,** 31)

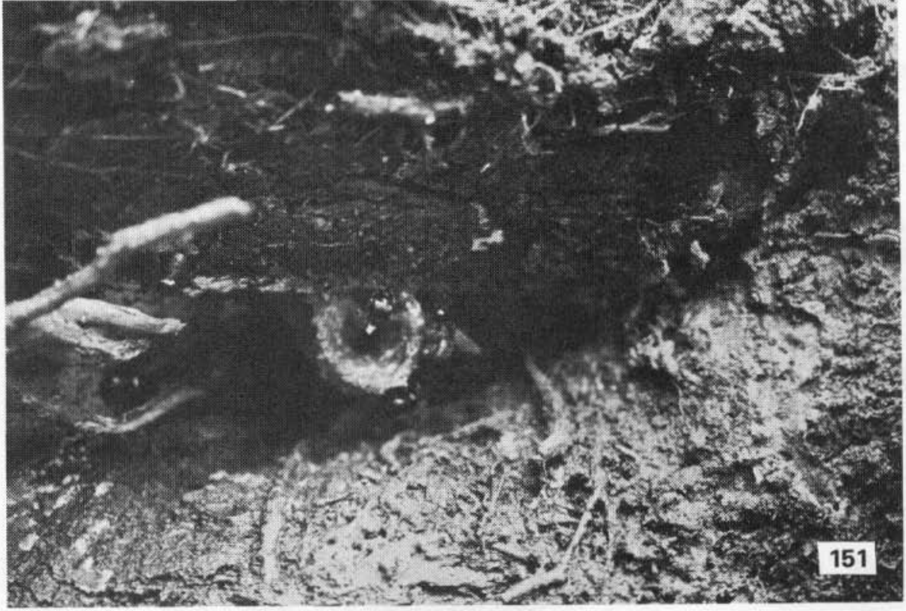
T. nebulata komiensis: 195–2000 (**Darchen,** 11)

T. schrottkyi: 300 (**Ihering,** 18, 21)

T. iridipennis: 2250 (**Schulz,** 58)

Figure 151. *Melipona flavipennis* (*sp.* 128), nest entrance.

Figure 152. *M. flavipennis* (*sp.* 128), nest exposed, showing pots at left and involucrum.



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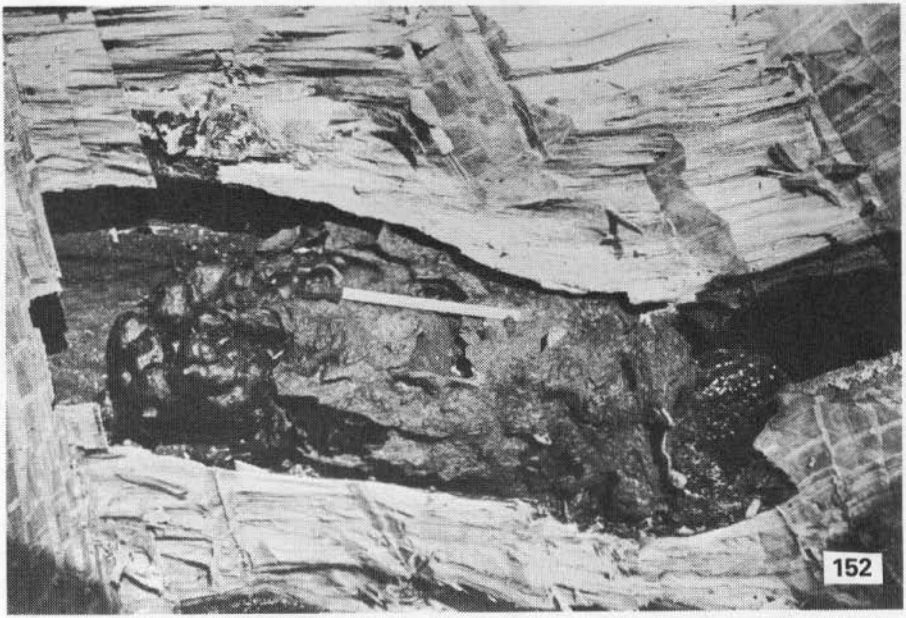

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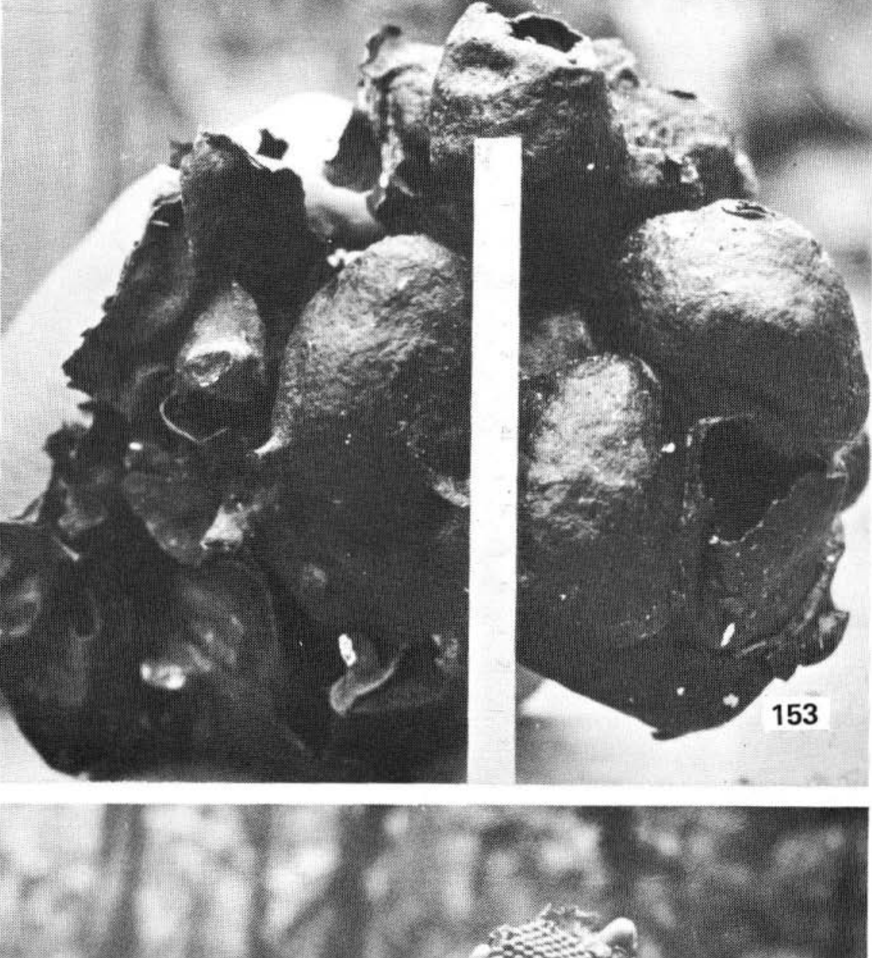
Figure 153. *M. flavipennis* (*sp.* 128), storage pots.

Figure 154. *Melipona marginata carrikeri* (*sp.* 133), top view of combs.



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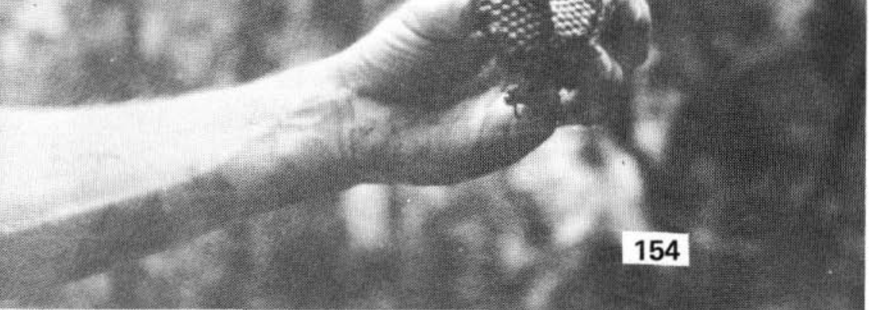

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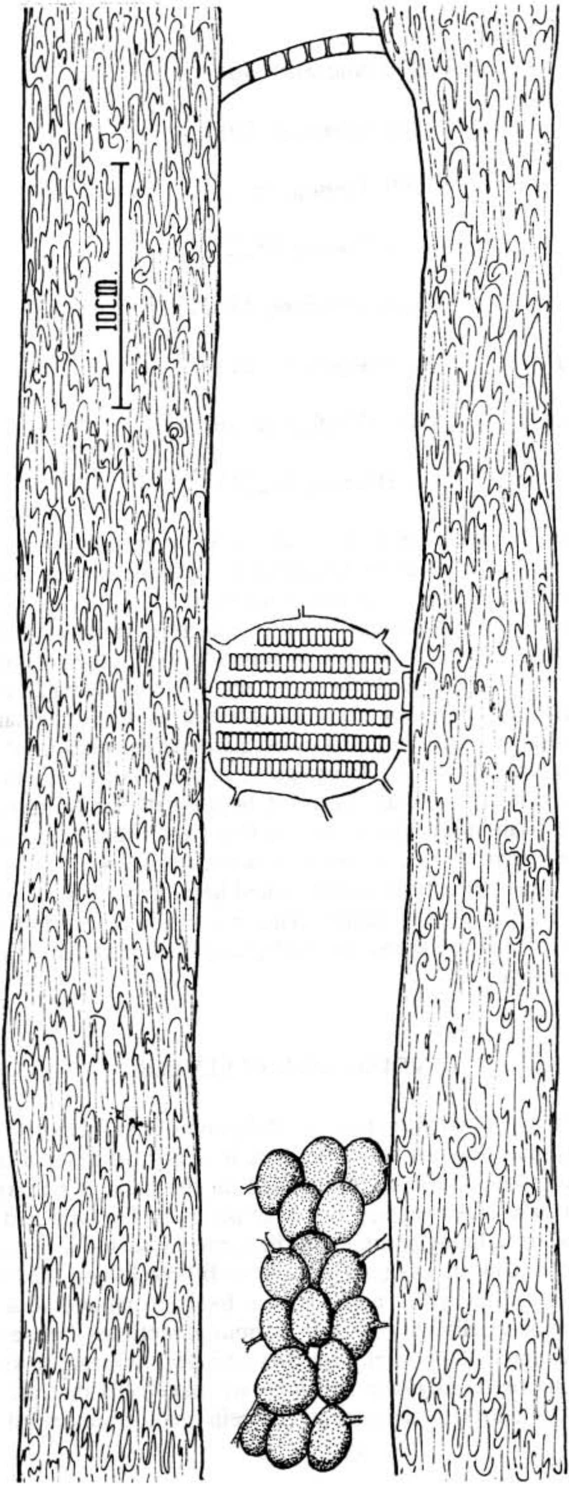
Figure 155. *M. m. carrikeri* (*sp.* 133), diagram of nest.



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T. cupira:	2900 (**Michener,** 30)
T. corvina:	7200 (**Michener,** 30)
T. spinipes:	5500 (**Ihering,** 18, 21)
T. mosquito:	1175 (**Ihering,** 18, 21)
T. xanthotricha:	24, 423 (**Ihering,** 18, 21)
M. m. marginata:	243 (**Ihering,** 18, 21)
M. m. marginata:	160–170 (**Schulz,** 56)
M. anthidioides:	894 (**Ihering,** 18, 21)

Beside these data, claims of populations up to 200,000 seem outlandish. But the nest of *T. corvina* listed above had some 82,000 cells and cocoons; more adults may have escaped than seemed possible at the time.

Another attribute recorded in Table 6 is aggressiveness of the bees when the nest is disturbed. Of course there is some variation within the categories used in the table. *T. cupira* and *corvina* seem the most aggressive of all, while *T. guatemalensis* is among the less aggressive of those categorized as 4. Yet remarkably enough, considering its small size and gentle relatives, *guatemalensis* is a most unpleasant bee to work with, as are all those in its category. In the amount of damage done to its attackers, *T. tataira* is in a class by itself because of the burning and blistering compounds in its mandibular glands, but its flight and other behavior patterns seem no more aggressive than those of other species in category 4.

The other nonarchitectural feature noted here, also recorded in Table 6, is the reaction of the authors to the honey. This is a crude record but until studies of water content and chemistry can be made, such data may have some value, even though very subjective.

EVOLUTIONARY LEVELS

Unfortunately the architecture of Meliponini is sufficiently different from that of other Apidae that for most features it is not possible to determine what conditions are ancestral and what are derived on the basis of similarities to related groups. One can only make guesses. For example, both *Euglossa* and *Bombus* make batumen-like layers, a lining batumen in the former case and a waxy sheet over the nest in the latter, and even *Apis* uses propolis to fill cracks and the like. Therefore a single batumen layer lining the nest cavity is likely to be ancestral in Meliponini. *Euglossa* often makes cells with axes in various directions. Hence this feature is likely to be ancestral in Meliponini. (*Bombus* and *Apis* cells are so specialized as to contribute nothing here.) *Euglossa* and *Bombus* make cells that are not in combs, suggesting that the cluster arrangement of cells may be ancestral in Meliponini.

Table 6: **Observations on nest populations, honey and aggressiveness of some Costa Rican Meliponini. (Aggressiveness is recorded according to the following scale based on responses when the nest is opened: 1, timid, not aggressive; 2, a few fly out and bite; e, many fly out but few bite; 4, many fly out and bite).**

	Population	Honey	Agressiveness
12. *T. frontalis*	1900	sweet, rather acid, pleasant	1
18. *T. pseudojatiformis*		sweet, slightly acid, yellowish, good	1
21. *T. tica*		sweet, slightly acid, viscous, good	1
22. *T. mirandula*	2281–4076	sweet, slightly acid, viscous; good or acid, bitter, fluid, not pleasant	1
29. *T. atomaria*	500		
30. *T. buyssoni*	136+		
34. *T. rhodopta* = SP. B	5058	very bitter	
35. *T. latitarsis*	393	sweet, pleasant, viscous	1
39. *T cupira*			4
42. *T. testacea musarum*			4
45. *T. guatemalensis*		sweet, rather watery, good	4
49. *T. ornaticeps*		sweet, scarcely sour, good	1
51. *T. p. peltata*		sweet, not sour, viscous, good	2
55. *T. mexicana subobscuripennis*		sweet, slightly acid, fluid	3
61. *T. mellaria*		very watery, acid (like lemonade)	1
62. *T. testaceicornis perilampoides*		sweet, viscous, neither acid nor bitter	1
64. *T. capitata zexmeniae*		sweet, rather acid, viscous, good	1
67. *T. tataira mellicolor*		acid to sweet, moderately viscous	4
71. *T. buchwaldi*	1326 2979	acid, watery	1
75. *T. dorsalis*		very acid	2
85. *T. j. jaty*		sweet to somewhat acid, viscous, good	1
90. *T. nigra paupera*		sour, bitter, watery	1
91. *T. perangulata*		sour, watery	2
101. *T. corvina*		sour, sometimes slightly bitter, watery	4
105. *T. f. fulviventris*		sweet, viscous, slightly acid, good	1
107. *T. fuscipennis*		sour, watery, worse than that of *corvina*	4
111. *T. nigerrima*		bad tasting, not sour or viscous, salty and bitter	3
119. *L. limao*		mixed with pollen	1
124. *M. f. fasciata*		sweet, slightly acid, watery	1
125. *M. fasciata melanopleura*	2000	sweet, watery	1
133. *M. marginata carrikeri*	210	sweet, not sour, viscous, good	1

The problem is that none of these features is complex enough or sufficiently intricately related to others to provide any assurances against convergences or reversions.

Indications of ancestral architectural attributes can also come from relations to morphological attributes of adults. Wille has shown, by comparison with other bees, that of the Meliponini, the *Trigona* subgenera *Plebeia, Nogueirapis* and *Hypotrigona* have maximum numbers of ancestral features in adult morphology. Moreover the mid–Tertiary fossils that have been adequately studied belong to *Nogueirapis* and the *Hypotrigona* group (**Kelner–Pillault,** 23; **Wille** and **Chandler,** 76). Therefore one can reasonably look for ancestral architectural features in these same groups.

Using the symbols of Table 4, the following paragraphs show probable ancestral states for those characters where appropriate evidence exists; then indications of derived states are shown in parentheses by arrows. Two–headed arrows suggest that there may have been evolutionary reversals. Numbers correspond to those of Table 4 and the explanation of the symbols is as for that table. Omitted numbers represent characters for which we have no idea of the evolutionary direction. Asterisks indicate characters that are used below in judging evolutionary levels.

1.* Length of external entrance tube: –(→ + ↔ → + +). No other apids make external tubes. Hence their absence is probably primitive. The two–headed arrow, however, shows our belief that they can decrease as well as increase in size, perhaps with changes in the need for defense, inconspicuousness, or recognizable landmarks.

2.* Shape of external entrance tube: $C\left\{\begin{array}{l}(\to F)\\(\to T)\\(\to I)\end{array}\right.$. Neither funnel–shaped nor tapering entrances are common in the supposedly primitive groups listed above. For this reason as well as because of the simplicity of the cylindrical construction, we consider it ancestral and the others derived from it.

3, 4. Hard entrance tubes, especially those hard to the apices, are derived, and lack of ornamentation is presumably ancestral. Like length, these are probably features that can evolve in either direction and are not likely to define groups.

8.* Radiating ridges around entrance: –(↔ + → + +). These ridges are found chiefly in certain species of *Melipona* and not in the groups thought to be primitive.

9. Size of entrance: ++ must be deroved but which of the others is ancestral is unknown.

10. Sometimes with two or more entrances: – (→ +). This feature is so plastic as to be of little use.

12.* Number of layers of batumen: 1 (→ several ↔ many)

12a.* Nest location (see Table 2): In cavity (→ partially exposed → exposed). Most other apids nest in cavities and primitive Meliponini presumably did so also.

15.* Plant or fecal material or mud in outer layers of exposed batumen. –(→ +). This is a feature of some of the species making exposed nests and is doubtless derived.

17. Number of layers of involucrum: $1 \left\{ \begin{matrix} (\rightarrow 0 \leftarrow \\ (\leftrightarrow \text{several} \end{matrix} \right\} \leftrightarrow \text{Many}).$ Same as for 12, but may revert to O.

20.* Shape of honey pots: S or E (→ L). See 21.

21.* Shape of pollen pots: S or E (→ L). Long storage pots are found only in certain species of *Tetragona* and in *Trigonisca*, both groups with various derived morphological characters.

21a.* Separation of storage pots: Well separated (→ fused). It seems reasonable to suppose that separated pots like those of *Trigonisca*, at least *T. buyssoni*, are more primitve than the fused pots of other *Trigona*. *Melipona* may be intermediate. The degree of fusion depends so much on the density of pots relative to available space and food that this character has not been used here or in the tables.

25.* Shape of brood cells: S or Ss (→ E↔ L). Spherical or nearly spherical forms are found in Australian *Plebeia* as well as in some American forms, none with numerous specialized group features.

25a.* Orientation of cells: Axes in various directions(→ Axes at right angles to comb). This feature has not been recorded for most cluster makers but we believe that varied axis directions occur only in Australasian *Plebeia* and in *Trigonisca*.

25b.* Queen cell size: Large (→ equal in size to worker cells). Small queen cells are associated with the partially genetic caste determination of *Melipona*, almost certainly a derived feature in any social insect group.

26.* Arrangement of brood cells: $C \left\{ \begin{matrix} \longleftarrow \\ (\longrightarrow CL \end{matrix} \right\} \left\{ \begin{matrix} \leftrightarrow IC \leftrightarrow Co \leftrightarrow SC) \\ \rightarrow VC) \end{matrix} \right.$ Unstructured clusters of cells oriented in varying directions are believed to be the ancestral condition, found in Australian *Plebeia (australis)* and in *Trigonisca*. The Australasian *Plebeia (cincta)* with the CL arrangement also has cells opening in various directions. Perhaps the spherical cells of the two *Plebeia* species listed are more primitive, as **Michener** (32) suggested, but what we now know of cells of *Trigonisca* leaves one in doubt. *Trigonisca* has oval cells. By and large, elongation of cells should be associated with crowding and with uniform orientation, such as is found in the IC, Co, and SC arrangements. The Australian *Plebeia* (C) as well as the Australasian *Plebeia* (CL) live in moderate sized cavities and establishment of orderly cell arrangements through the series IC —> Co and SC established the necessity for such cavities. Nesting places being at a premium, however, reversion to C, especially in small species, should be advantageous as, along with loss of the involucrum, it permits the use of small and irregular or tubular nest cavities. The BC and IS arrangements must be early stages in such disorganization. This reversion, loss of cell organization, appears to have occurred several times, for vertically elongated cluster cells occur without the involucrum in some species of *Plebeia*, *Scaura*, *Tetragona*, and *Lestrimelitta* as well as all species of *Hypotrigona* and *Trigonisca*. Because of the disorientation now known in *Trigonisca* cells, one wonders if its cell arrangement is primitive or a result of breakdown of combs; its relation to the primitive *Hypotrigona* may suggest that its cell arrangement is primitive. However, for calculations about evolutionary levels, we have considered it derived and regard

Table7: Percentage of ancestral character states out of total number of applicable characters for several meliponine species.

	N^{o} of applicable characters	% ancestral states
7. *T. australis*	13	85
12. *T. frontalis*	12	75
21. *T. tica*	13	61
22. *T. mirandula*	12	92
34. *T. rhodopta*=SP. 8	10	70
51. *T. peltata*	14	50
85. *T. jaty*	14	64
90. *T. nigra*	11	73
101. *T. corvina*	15	53
116. *D. staudingeri*	14	50
119. *L. limao*	13	54
124. *M. fasciata*	12	50

as primitive only the cluster makers that also make involucra. The single VC meliponine, *Dactylurina,* presumably illustrates an entirely separate evolution of cell arrangement perhaps starting from CL. Our objection to the theory that all the cluster arrangements are ancestral to comb arrangement is that this would have required repeated evolution of the rather complicated horizontal comb, at least once for each group listed above as having both comb and cluster making species. It is more reasonable to hypothesize one origin of vertical elongate cells and horizontal combs, and repeated breakdown of this arrangement, following **Michener** (32) and **Wille** (75). The presence of some cluster making species (sometimes called *Frieseomelitta)* in the specialized subgenus *Tetragona* is one of the problems in regarding cluster making as always ancestral.

28.* *Pillars in brood chamber:* $S\left\{\begin{matrix}(\rightarrow L)\\(\rightarrow LL)\end{matrix}\right.$. The short temporary pillars, from one comb to the next, are found throughout the group. Only two evidently specialized types have long permanent pillars, one type (LL) being found in the subgenus *Partamona,* the other in some species of the subgenus *Trigona.*

All forms probably have a mixture of ancestral and derived attributes. It would be of interest to learn which groups or species have the maximum numbers of each. However, because of plasticity and consequent variability in the expression of characters, and the small number of architectural characters, it is not possible to progress far along such lines or to develop a phylogeny based on the architectural characters. It is important for students of these bees to remember that possession of an ancestral character does not indicate that the bee is primitive. The bee may be primitive in that character while many of its other features are derived. Erroneous wording and probably thinking have pervaded certain accounts of lines of descent among Meliponini.

To give an idea of evolutionary levels indicated by combinations of characters, representative species have been selected (Table 7). Using the characters marked with asterisks (*) in the above list, the percentage of ancestral features out of the total number of applicable features for each species has been calculated and appears in the table. Because of the large and variable numbers of inapplicable (NC) characters (no comparison, e.g., characters 2, 3, and 4 above cannot be used to compare forms lacking entrance tubes), one cannot meaningfully compare numbers of ancestral attributes of one species with those of another

In gathering data for the figures in Table 7, a character having an intermediate level of derivation for a given species was omitted for that species. Of course there may be several derived states. Thus for character 2, F, T, and I are all derived. For character 17, 0 and several to many are both considered derived; for 25, E and L are considered derived; for 26, CO and SC as well as VC are considered derived, as is C when associated with oval cells. When Table 4 shows variation in a character for a species, the more derived state was used in preparing Table 7.

The table shows higher percentages of primitive architectural characters, in general, in the morphologically primitive groups. In view of the partly circular methodology (some architectural characters were judged to be primitive because they are possessed by morphologically primitive bees), however, we do not wish to emphasize this aspect of the study at this time.

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ADDENDUM

After this paper was in proof we received copies of other pertinent papers as follows: Darchen, 12a, 12b, and Nogueira–Neto, 41a.

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ERRATA

Page 10, line 12, second column, for *"Meliplebeia tanganyika"* read *"Meliplebeia tanganyikae"*

Page 25, last line, for *"T. dallatoreana"* read *"T. dallatorreana"*

Page 28, last line, for *"incolved"* read *"involved"*

Pages 64, 66. 67, 69, 72, table 5, heading of column 2, for "Post (mm)" read "Pots (mm)"

Page 77, line 1, for "showr" read "shown"

Page 97, figure 5, for "Cells of *T. (P). australis*" read "Cells (left) and pots (right) of *T. (P) australis*"

Page 99, line 15, for "comb" read "combs"