PSYCHE

Vol. 101 1994 No. 3–4

NEST ARCHITECTURE OF THE AUSTRALIAN PAPER WASP *ROPALIDIA ROMANDI CABETI,* WITH A NOTE ON ITS DEVELOPMENTAL PROCESS (HYMENOPTERA: VESPIDAE)

BY SÔICHI YAMANE[1] AND YOSIAKI ITÔ[2]

ABSTRACT

Nest architecture of *Ropalidia romandi cabeti* was described, based on 2 incipient (an active and an abandoned) nests and 3 developed ones. Developed nests were spherical, or hemispherical when built under flat surfaces, consisted of several to more than 10 horizontal combs with oval or irregular shapes. Each comb was suspended by many pedicels from the upper one. Since several combs were simultaneously constructed at the same story, they often produced irregular interconnections that caused complex stair-like, or "semispiral" structures. Combs were entirely surrounded by an outer envelope with a small entrance hole at the lower tip. The envelope was probably constructed after the first group of combs had been completed. Materials for both cells and envelope were plant fibers glued together with salivary secretion. The surface of envelope was more thickly coated with the secretion than cell walls. The largest nest had about 30,000 cells in more than 10 stories of combs that had a surface area of 1,933 cm^2. Its dimensions were 21.5 cm in longer diameter and 17.5 cm in height.

[1] Biological Laboratory, Faculty of Education, Ibaraki University, Mito, 310 Japan
[2] School of Arts and Sciences, Okinawa University, Kokuba, Naha 902, Japan
Manuscript received 14 March 1994.

INTRODUCTION

The genus *Ropalidia* is endemic to the Old World including Oceania, and is one of the largest polistine genera, comprising nearly 130 species (Richards 1978). This genus is unique within the subfamily Polistinae in containing both independent- and swarm-founding species (Jeanne 1980). The majority of the former group (subgen. *Icariola* of Richards 1978, etc.) have relatively small colonies and construct uncovered nests, while the latter (subgen. *Icarielia,* etc.) have large colonies and covered nests. Architecture of *Ropalidia* nests has been described by some authors (Carl 1934, Vecht 1962, Richards 1978, Yamane and Yamane 1979, Kojima 1982, Kojima and Jeanne 1986). Kojima and Jeanne (1986) discussed evolutionary radiation, focusing on the subgenus *Icarielia* which mostly build multiple combs entirely covered by an envelope.

As part of comparative studies of nest architecture in *Ropalidia,* the present paper describes nests of a swarm founder, *R. (Icarielia) romandi cabeti* (de Saussure), which is one of the commonest species in Queensland (Qld), Australia. A developed nest of this species was photographed by McKeown (1942), and the gross nest architecture was described by Richards (1978) based on one vacated and two active nests collected in Qld. This paper adds more detailed data based on quantitative and SEM observations, and outlines a possible developmental process of a nest.

MATERIAL AND METHODS

Nest RM841 and nest RM861 were collected at the same site under the eaves of a concrete building of the School of Australian Environmental Studies, Griffith University at Nathan, Qld on 4 September 1984 and 3 October 1986, respectively. Another nest, RM862, was collected among branches of a mango tree in the garden of CSIRO on the Atherton Tableland, Qld on 13 October 1986. For these nests, the outer and inner structure and population parameters were examined. An incipient nest, RM871, being just in the process of founding by a swarm, was observed on a palm leaf on 15 and 16 September 1987 in Cairns, Qld. In addition to these nests, the remains of an abandoned incipient nest (RM863) were

observed under the eaves of the building of the Tropical Forest Research Centre, CSIRO at Atherton on 13 October 1986.

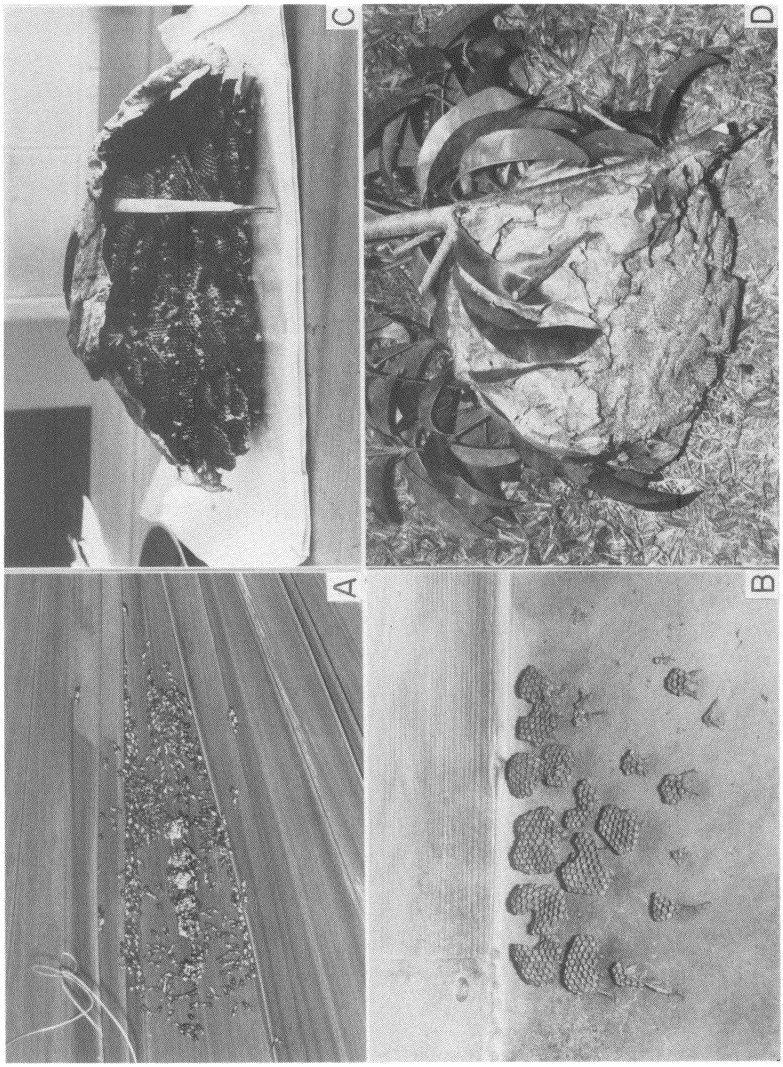
Nests RM841 and RM862 were dissected to count the numbers of combs and of cells and cocoons in each comb, and to estimate the surface area of combs. To measure the surface area the shape of each comb was traced on paper, then cut-out pieces of the paper were weighed to 1 mg with an electronic balance and their areas were calculated to 0.1 cm^2 by multiplying the recorded value by the area/weight factor. The number of cells per comb was also estimated by applying the number of cells per weight of paper. To obtain the number of cells per weight of paper, four combs and one comb were selected from RM841 and RM862, respectively. Nest RM861 was also dissected, and the number of cells was directly counted. Number of cocoons was directly counted for all the nests, but those of larvae and eggs were not censused. Some pieces of carton were cut out from envelopes and cells for a SEM (Nihon-Denshi Co., JSM-T20) observation. To make plant fibers visible from outside, the salivary coat on the surface was removed by immersing the nest pieces in a 0.5N KOH solution for 5–7 hours.

Results

1. Incipient nests

RM871 (Fig. 1A): A swarm of wasps was found on 15 September 1987 on the underside of a large palm leaf at about 2.5 m above the ground. At 1430 h it consisted of more than two hundred wasps covering a round comb of 15 mm in diameter attached by a short pedicel to the substrate. This suggested that the swarm had arrived at the place within the previous few days. Three additional combs were made by 1630 h. At 0950 h on the next day the nest had 6 combs that were linearly arranged along 10 cm of a vein of a leaf. Each of these combs had 20 to 30 cells, and the outer envelope was not yet constructed. Whether the cells had received eggs was unknown. There were 215 wasps on and around the combs, suggesting that the swarm consisted of more than 250 wasps, since many individuals were probably performing in extranidal activities.

RM863 (Fig. 1B): This abandoned nest consisted of 14 empty combs, excluding those with a single cell or consisting only of a pedicel. These combs were built within a square range of 12.5 ×


A
B
C
D

8.5 cm and had as yet no sign of envelope construction. Four developed combs had been fused together into two larger ones. The shape of the combs varied from nearly round to C-shaped, and most combs were attached to the ceiling with multiple pedicels. The largest comb had about 70 cells and the total number of constructed cells was estimated at about 450.

2. Developed nests

RM841 (Fig. 1C, 2A): A medium-sized and probably matured nest was collected together with nearly 5,900 adult wasps, involving multiple queens, workers and males, under the eaves of a concrete building at about 2.5 m above the ground.

Gross architecture: The nest was a slightly compressed hemispheroid, consisting of more than 8 horizontal combs, which were interconnected with many ribbon-like pedicels and were entirely covered with an envelope. The diameter of the nest at the base (including envelope) was 29.0 × 20.0 cm and the height was 12.5 cm. The number of cells was estimated at 23,880 in more than 8 combs, and the total comb area was about 1,570 cm^2 (Table 1).

Envelope: As in most *Ropalidia* nests, the envelope consisted mostly of single-layered (partially double-layered) lamina, made from carton (a matrix of plant fibers and fragments), of unknown origin. According to SEM observations, the material contained long single fibers, imperfectly split fibers, and non-fibrous matter. Some non-fibrous fragments were thin and had regularly arranged minute pores (Fig. 3B). Both sides of the lamina were so thickly coated with wasp saliva that the fibrous structure was almost invisible (Fig. 3A). Color of RM841 was uniformly light gray, suggesting that wasps foraged for the materials from the same kind of source. The envelope was constructed independently of combs, but connected to some upper combs with ribbon-like pedicels. It was not imbricate but weakly waving all over the surface. A round entrance hole (10 × 7 mm in diameter) opened at the bottom tip.

Fig. 1. Nests of *Ropalidia romandi* at various developmental stages, all of which were collected or observed in Queensland. A: Incipient nest (RM871) just founded underneath a palm leaf (15 September 1987, Cairns), B: Abandoned nest RM863 which was not covered yet (13 October 1986, Atherton), C: Medium-sized nest RM841 built under the eaves of concrete building (4 October 1984, Nathan), D: Nest RM862 built among branches of a mango tree. Lower combs are disclosed after collection (13 October 1986, Atherton).

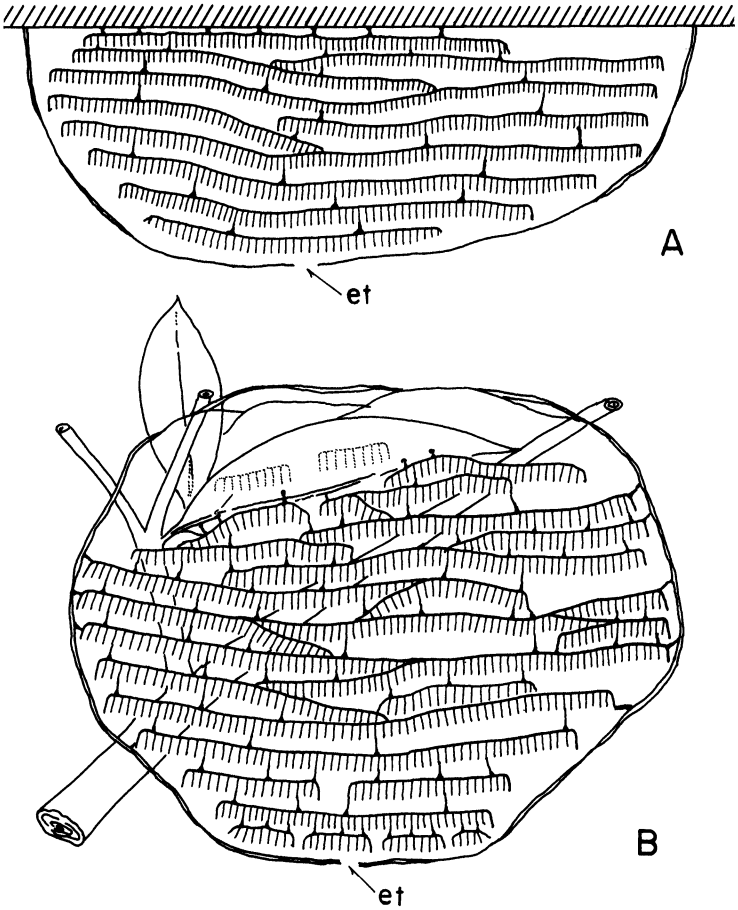


Fig. 2. Vertical sections of 2 mature nests of *Ropalidia romandi*. A: RM841 built under the eaves, and B: RM862 built among branches of a mango tree. Irregular connections of combs that demonstrate a "semispiral" structure are seen at the upper part. et: entrance hole.

Combs and cells: Combs were horizontal and flat, but occasionally uneven combs were caused by spatial and other factors such as fusion of neighboring combs. Combs even at different stories were often interconnected and produced a complex stair-like structure

Table 1. Comb and cell composition of nest RM841 collected on 4 October 1984 at Griffith Univ., Nathan.

Combs*	No. cells	No. petioles	No. cocoons	Area (cm^2)
1	2,967	21	61	195
2	3,750	20	599	247
3	4,740	17	659	312
4	4,486	11	853	295
5	3,310	14	537	218
6	2,593	8	323	171
7	1,577	5	86	104
8a	205	1	0	14
8b	254	1	0	17
Total	23,882	98	3,118	1,573

* Number means the story of comb(s). The lowest story had 2 combs (8a and 8b).

(Fig. 2A). Such a structure, as well as irregular comb shape, was mostly a result of simultaneous initiation of more than one comb at the same story. Each comb was suspended from the one above by many (20 in second comb) pedicels, most of which were broad, ribbon-like and very tough. The basal combs were always attached to the substrate with pedicels. The largest comb (third comb from the base) had the dimensions of 28.0 × 16.0 mm, with a comb area of 300 cm^2 and 4,550 cells (Table 1). Cells were mostly hexagonal and regularly arranged, but those located where two neighboring combs met were irregular. Like other species of *Ropalidia* and *Parapolybia* of the Old World, cells which once had pupae had a small round hole (window) at their bottoms, which was in most cells sealed with a transparent membrane made from saliva. The mean diameter of cells at their mouth measured as distance between the opposite sides was 2.3 mm (S.D. ±0.2 mm, n = 10), and did not fall into different size types. Judging from the distribution of pupae and windows, two bottom combs had not yet produced adults. The fine surface structure of cell walls was similar to that of the envelope (Fig. 3C, D). Cocoon cappings were white, delicate, and domed, protruding 1 mm beyond the cell mouth. The surface of their tops was not daubed with carton.

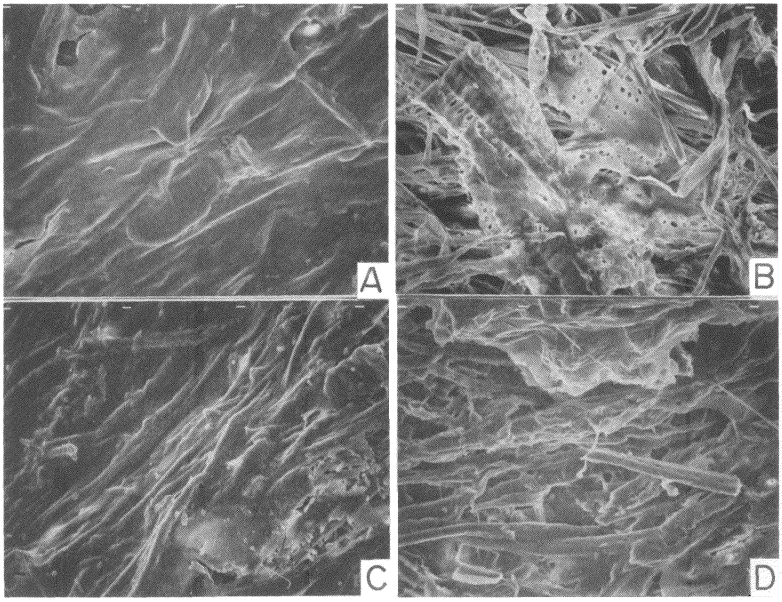


Fig. 3. SEM enlargements of the envelope and cell wall. A: Outer surface of envelope from an arboreal nest, B: Same as A. Salivary coat was removed to expose fibrous structure. C: Surface of cell wall, and D: Same as C, exposed.

RM861: This nest was collected in 1986 at the same site as for RM841, but judging from its small size, it was probably not reconstructed by wasps of RM841 that escaped during the collection in 1984. The nest contained thousands of wasps with multiple queens. The structure was essentially the same as that of RM841, except that all combs were horizontal and flat, and mutually unconnected. Most of the envelope was double layered and an entrance hole opened at its bottom. The color was the same as in RM841. The nest had a total of 5,613 cells (1,306 cocoons) in 6 combs (Table 2).

RM862 (Fig. 1D, 2B): This nest was built among branches of a mango tree and was the largest among those collected in the present study. It had more than 5,000 wasps, including multiple queens. The architecture was slightly modified, affected by the substrate to which it was attached. The nest was spheroid with a diameter of 21.5 cm and a height of 17.5 cm (including envelope).

Table 2. Comb and cell compositions of nest RM861 collected on 3 October 1986 at Griffith Univ., Nathan

Combs	No. cells	No. petioles	No. cocoons
1	1,973	8	412
2	1,402	6	263
3	910	7	320
4	697	5	241
5	490	4	70
6	141	1	0
Total	5,613	31	1,306

The envelope consisted of double (partially single) layers of laminae. The top of the nest was round, with no particular structure of reinforcement against rains, such as a roof cone seen in vespine nests (Yamane, 1992). Instead, nine mango leaves (ca. 12 cm long and 4 cm wide), which were incorporated into the envelope, completely covered the nest top. Color of both envelope and cells was creamy brown.

The nest consisted of more than 28 combs in 10 stories. The number of combs was not exactly counted because of many irregular connections, and complex comb arrangement especially in the upper half of the nest (Fig. 2B). This apparently resulted from the building of the nest on an uneven surface. The first comb was probably built on the underside of a mango leaf. The shape of combs was very irregular. Total comb area was estimated at 1,933 cm^2, and the number of cells at 30,010, of which 4,310 had cocooned stages (Table 3).

Discussion

Our observations on the architecture of *R. romandi* nests are consistent with the description by Richards (1978) and a schematic representation by Kojima and Jeanne (1986: Fig. 7I) of the same species. Richards (1978) stated that in the upper half of a big nest, which had about 130,000 cells in approximately 17 combs, much of the structure was semispiral. In the case of our nests, such a trait was recognized only in RM862, that was built among tree branches. This type of "semispiral" structure is also seen in *R.*

Table 3. Comb and cell compositions of Nest RM862 collected on 13 October 1986 at CSIRO, Atherton.

Combs*	No. cells	No. cocoons	Area (cm^2)
0a	78	0	5
0b	59	0	4
1a	233	81	15
1b	158	34	10
1c	244	24	16
1d	269	50	17
1e	51	13	3
1f	1,186	76	76
2	1,115	44	72
3	1,771	36	114
4	2,619	228	169
5a	2,034	243	131
5b	318	69	20
6	2,804	359	181
7a	4,239	535	273
7b	104	0	7
8	4,410	738	284
9	978	302	63
10	2,957	600	190
11a	2,047	550	132
11b	334	80	21
12a	275	13	18
12b	376	95	24
13	984	140	63
14a	79	0	5
14b	181	0	12
14c	37	0	2
14d	69	0	4
Total	30,010	4,310	1,933

* Number means the storey at which combs (a, b,....) were situated. Combs at story-1 were probably built first, and small combs at story-0 were built later at spaces above story-1.

montana (Kojima and Jeanne 1986). It is not identical to the true spiral type, which is seen in *Polybioides raphigastra* (Vecht 1966) and *Agelaia areata* (Wenzel 1991, cited as *Stelopolybia areata*: Jeanne 1973), at least the latter of which constructs nest by sessile cell initiation on the substrate. To realize a true spiral, wasps must

always add new cells at one advancing front. The semispiral in *R. romandi* and *R. montana* seems to be realized mostly by irregular interconnections of combs that were initiated simultaneously at several points on an uneven surface. Carl (1934) and Wenzel (1990) regarded *R. montana* as making helical combs, but these combs are not truly spiral in the above sense. In vespines, usually a single new comb is initiated at a given story, mostly at the center of the upper comb, and such a manner tends to preclude semispirals (Matsuura and Yamane 1991, Yamane 1992).

The nest architecture of *R. romandi* is essentially similar to that of other species of subgenus *Icarielia* so far observed (Kojima and Jeanne 1986). Each comb is simple, and as in the genus *Polistes* and other polistine genera endemic to the Old World (*Parapolybia, Polybioides* and *Belonogaster*), it never builds double-sided combs with cells opening to the opposite directions and sharing a common base. One reason for this may be a meconium extracting habit of adult wasps in these taxonomic groups (Jeanne 1980, Kojima and Jeanne 1989). Wenzel (1991), however, stated that there are over 600 New World polistine species, none of which remove meconium through the back of the cell, and yet only two species (*Agelaia lobipleura* and *Mischocyttarus pelor*) build double-sided combs (Wenzel 1991). He, therefore, considers that there is some phylogenetic constraint separate from the hygienic behavior that prevents them from experimenting with double-sided combs.

The absence of two size-types in cells may reflect weak morphological caste differences in this species (Shima et al. unpubl.). It is also consistent with all the other *Ropalidia* species so far examined (Kojima and Jeanne 1984), except *R. ignobilis*, a Madagascar species. Although *R. ignobilis* dwells in small colonies, it exceptionally has pronounced morphological castes (Wenzel 1992). The occurrence of two size-types in cells is common in the subfamily Vespinae (Yamane 1992).

SEM observations showed that the entire surfaces of nests were coated with salivary secretion, but the coating was thicker in a nest built on a tree than those built at sheltered sites. The thickness of the salivary coat might be related, at least partly, to the amount of rain to which the nest is exposed. If this is true, wasps nesting at places or localities having heavier rains must invest more in pro-

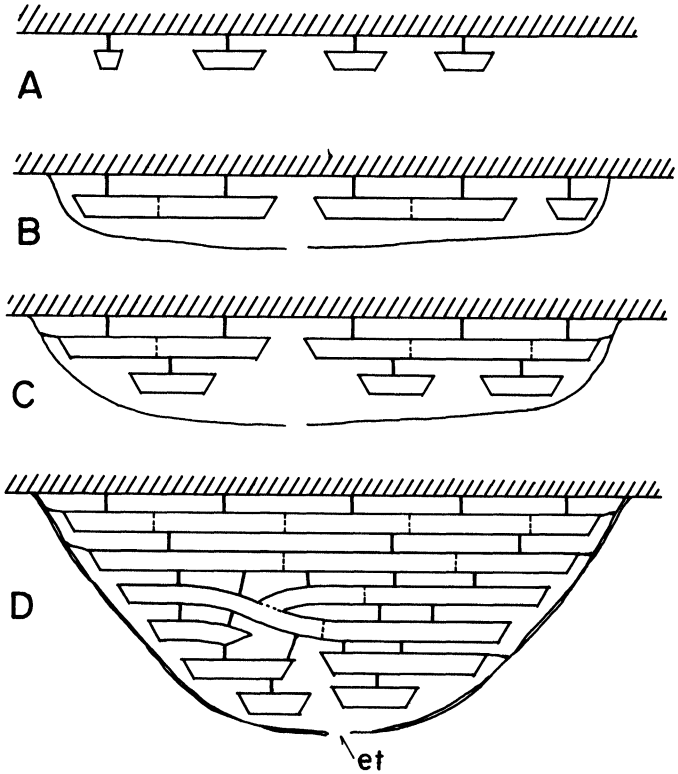


Fig. 4. Estimated ontogenetic development of a nest of *Ropalidia romandi*. A: Uncovered stage, B: Covered, single-storied stage, C and D: Multiple-storied stage. et: entrance hole.

ducing saliva, which involve proteinous elements as shown in *Polistes metricus* (Singer et al. 1992).

Based on the present observations of nest architecture, the ontogenetic development of a nest in *R. romandi* is tentatively estimated as follows: (1) Several combs are simultaneously initiated prior to envelope construction (uncovered stage, Fig. 4A). (2) As the combs are expanded, they are fused together at their growth fronts and, thus, produce larger combs. In the case of our nests, the

envelope had not yet been constructed at this stage. In contrast, Kojima (pers. comm.) observed that in some nests of this species the envelope was constructed soon after the first comb was initiated. One of us (Y.I.) observed an early nest of this species in 1993, and noted that it had not yet had the second storey of combs, but the envelope had been partially constructed (covered single-story stage, Fig. 4B). These observations suggest that the timing of envelope initiation varies across individual nests, particularly the swarm size. (3) More combs are then added downwards, and the envelope is expanded and modified as the combs grow (multiple-story stage, Fig. 4C, D), as seen in some species of *Parachartergus* and *Pseudopolybia* (Wenzel 1991). This process differs from that seen in *R. extrema,* an *Icarielia* species distributed in the Philippines. In *R. extrema a* full-sized envelope seems to be constructed soon after initiation of the first comb, and the combs at the bottom layer face upwards (Kojima and Jeanne 1986). The number of entrance holes was considered to be one in all the material examined, but it seems to vary with nest size and some other factors. S.Y. observed in Brisbane, Qld, a big nest constructed on the vertical wall of a house which had several entrance holes along the side.

Acknowledgments

We thank B. Jenkins and C. Catterall for their help at the nest collection. Cordial thanks are also due to J. Kojima, J.W. Wenzel, and J. Rienks for critical comments on the manuscript, and R.W. Taylor for arrangement of the present surveys. J. Kojima offered us fresh material from an arboreal nest of *R. romandi* for a SEM observation that was undertaken by K. Kudo. This work was supported in part by a Grant-in-Aid for International Scientific Research Program (Nos. 63043019, 0104109 and 05041087) from the Japan Ministry of Education, Science and Culture.

Literature Cited

Carl, J. 1934. *Ropalidia montana* n. sp. et son nid. Un type nouveau d'architecture vespienne. Rev. Suisse Zool. 41:675–691.

Jeanne, R. L. 1973. Aspects of the biology of *Stelopolybia areata* (Say) (Hymenoptera: Vespidae). Biotropica 5:183–198.

———. 1980. Evolution of social behavior in the Vespidae. Ann. Rev. Entomol. 25:371–396.

Kojima, J. 1982. Nest architecture of three *Ropalidia* species (Hymenoptera: Vespidae) on Leyte Island, the Philippines. Biotropica 14:272–280.

Kojima, J., and Jeanne, R. L.. 1986. Nests of *Ropalidia (Icarielia) nigrescens* and *R. (I.) extrema* from the Philippines, with reference to the evolutionary radiation in nest architecture within the subgenus *Icarielia* (Hymenoptera: Vespidae). Biotropica 18:324–336.

McKeown, K. C. 1942. Australian insects: an introductory handbook. pp.190–191, Royal Zoological Society of New South Wales, Sydney.

Matsuura, M. and Yamane, SK. 1984. Biology of the vespine wasps. 323pp., 104 Figs., Springer-Verlag, Berlin.

Richards, O. W. 1978. The Australian social wasps (Hymenoptera: Vespidae). Aust. J. Zool., Suppl. 61:1–132.

Singer, T. L.; Espelie, K. E.; and Himmelsbach, D. S. 1992. Ultrastructural and chemical examination of paper and pedicel from laboratory and field nests of the social wasp *Polistes metricus* Say. J. Chem. Ecol. 18:77–86.

Vecht, J. van der 1962. The Indo-Australian species of the genus *Ropalidia (Icaria)* (Hymenoptera, Vespidae) (second part). Zool. Verhand.(Leiden) 57:1–72, 8 pls.

———. 1966. The East-Asiatic and Indo-Australian species of *Polybioides* Buysson and *Parapolybia* Saussure (Hym., Vespidae). Zool. Verhand. (Leiden) 82:1–42, 3 pls.

Wenzel, J. W. 1991. Evolution of nest architecture. pp.480–519, in Ross, K. G. and Matthews, R. W. (eds.), *The social biology of wasps,* Comstock Publ. Assoc., Cornell Univ. Press, Ithaca.

———. 1992. Extreme queen-worker dimorphism in *Ropalidia ignobilis*, a small-colony wasp (Hymenoptera: Vespidae). Insectes Soc. 39:31–43.

Yamane, Sô. 1992. A huge nest of *Vespa basalis* collected in Taiwan (Hymenoptera: Vespidae). Chinese J. Entomol. 12:1–11.

Yamane, Sô., and Yamane, SK. 1979. Polistine wasps from Nepal (Hymenoptera, Vespidae). Insecta Matsumurana (N.S.) 15:1–36.