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Nest Structure in Philippine Hornets (Hymenoptera, Vespidae, *Vespa* spp.)

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Abstract Nests are described from all four known Philippine *Vespa* spp., including the first described *V. philippinensis* nest. Specific features are related to nest-site habits of the species. Particular attention is given to the roof-cone and papering over of early combs in *V. affinis* nests, and the relative distinction of cell types and their distribution among the combs. Nest-site and structural data for these and other members of the genus are compiled in tabular form as an aid to further comparative study.

Introduction

The genus *Vespa*, comprising the true hornets, is native to Asia, Europe and North Africa, with one species introduced into North America (SPRADBERY, 1973; EDWARDS, 1980). Of the estimated 21 species in the genus, four are known from the Philippines (KOJIMA, 1982; KOJIMA & REYES, 1986). *V. philippinensis* SAUSSURE and *V. luctuosa* SAUSSURE are Philippine endemics, while *V. tropica* (L.) and *V. affinis* (L.) are widespread in East Asia (BEQUAERT, 1936).

Hornets produce colonies of a few dozen to several hundred individuals housed in nests of carton, a paper-like material. The brood-cells are grouped into horizontal combs, which are arranged parallel to each other and usually surrounded by a carton envelope with a single opening to the outside. The size frequency distribution of cells within a nest tends to be bimodal. Workers are consistently reared in small cells and queens in large cells, while males may be reared in either or both.

Within the scope of these common features, nests can vary in several ways between species and sometimes within species in different habitats (IWATA, 1976; EDWARDS, 1980; MATSUURA, 1984). In this paper we describe nest features of Philippine hornets and compare these with that is known from other members of the genus. Emphasis is on the nests of mature colonies, which have largely passed

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the stage of producing workers and entered into the final stage of producing males and new queens. At this time the nest has reached its definitive form, and differences between species are expected to be most pronounced.

Materials and Methods

All field observations from the Philippines are by one of us (CKS) during 1981–87. Other data are the responsibility of both authors. In addition to nests from known mature colonies, we utilize observations from some old nests which seem to be of about mature size and some from active colonies which had begun to produce males but not yet new queens.

Combs are numbered from the top, so that comb 1 is the earliest and uppermost in its nest.

Cells tend to be wider at the mouth than at the base, so that as the comb grows the peripheral cells come more and more to point away from the center (JANET, 1895, 1903). In some cases we utilize this tendency to identify the earliest part of a comb. Where one petiole was markedly stouter than the others, this provided an additional indication of the comb origin.

The cell-diameter measurement used here is between opposite sides of the cell, rather than opposite corners. In reporting diameters from authors who prefer the corner-to-corner measurement, we convert this by multiplying it by 0.87 (=sin 60°). Each of our diameter measurements is the mean from at least one row of 5–12 cells.

A cell with a cocoon or fecal pellet is recorded as having been utilized to rear at least one wasp. To estimate the number reared per cell, we took the standard approach (*e.g.*, YAMANE & MAKINÔ, 1977) of dissecting a sample of the cells and counting the fecal pellets.

Specimens of *V. affinis* from Palawan in the U. S. National Museum (USNM) and Visayas State College of Agriculture (ViSCA) identified by either author will serve as vouchers. Vouchers of the other three Philippine species can be recognized by their nest-series numbers as follows:

V. luctuosa, nos. 437, 848, 1195, 1221 and 1386, in the British Museum of Natural History (BMNH), Rijksmuseum van Natuurlijke Historie (RMNH), USNM and ViSCA.

V. philippinensis, no. 533, in the collection of Michael E. ARCHER (College of Ripon & York St John, England), University of the Philippines at Los Baños, USNM and ViSCA.

V. tropica, no. 1175, in the BMNH, RMNH and USNM.

Results

1. *Vespa tropica*

Direct observations are limited to six colonies in Camarines Sur and Sorsogon

provinces in southern Luzon. Each of these was in the soil in farmland. Underground nesting appears to be the almost invariant habit of this species in all parts of the Philippines. One evidence for this is CKS's failure to locate above-ground colonies on any of 11 islands on which *V. tropica* was seen flying, often abundantly. Another indication is the apparent common knowledge among local people that it nests in the soil, which is reflected in common names for the species. In Batangas province, for example, a distinction is drawn between *hilulumbo* ("hornet", *V. luctuosa*) and *hilulumbo-lupa* ("earth hornet", *V. tropica*). The nest-cavities examined appeared to be old rodent burrows.

The three nests excavated were all at Inang, Pilar, Sorsogon. All were in shallow burrows, about 10–20 cm below the surface, at edges of bamboo stands. The envelopes were thin, fragile and largely laminar, *i.e.* of mostly discrete sheets of carton. The largest of these apparently immature nests comprised four combs and about 450 cells. Combs were irregular in outline, with the upper surface curving downward away from the center, like a shallow inverted bowl. There was no fusion of combs, so that they were connected vertically only by petioles.

Cell diameters in the largest nest were 7.6–10.1 mm, with most in the range of 8.0–8.5 mm. In the largest comb there was a clear tendency for cells to become larger away from the center, but this was a gradual trend, without any clear distinction into two sizes. We presume that even the largest colony had not yet begun to rear queens. The cell walls appear quite thin in this species, though we have not measured this feature.

2. *V. philippinensis*

This seems to be the least abundant of the Philippine hornets and the one with the most restricted range. It is recorded from southern Luzon to northern Mindanao (KOJIMA, 1982; KOJIMA & REYES, 1986), but CKS has seen it only on Samar and Leyte, in the central part of its range, and even there it seems less common than either *V. tropica* or *luctuosa*.

The one nest examined was at ViSCA, Baybay, Leyte. It contained a healthy mature colony with 700 adults and ample brood (STARR, 1987). The nest was underground on a farm hillside (Fig. 1), and we suspect that this species typically nests in the soil. A pile of earth extended about 60 cm downhill from the burrow entrance, which was about 7 cm wide. The first part of the nest burrow was a nearly vertical, cylindrical tunnel, about 60 cm long and 10–11 cm wide (Fig. 1a). This opened into a cavity about 30 cm long and 25 cm wide, which in turn broadened into a cavity about 26 cm long (vertically) and 35–40 cm wide, with a surprisingly flat, horizontal floor (Fig. 1b). Our interpretation is that the wasps had modified an existing cavity by removing all loose earth from the tunnel and enlarging the burrow below as the nest grew. This would account for the pile of earth outside. The nest was contained in the second cavity and largely filled it. It was held in place by numerous roots which ran through it.

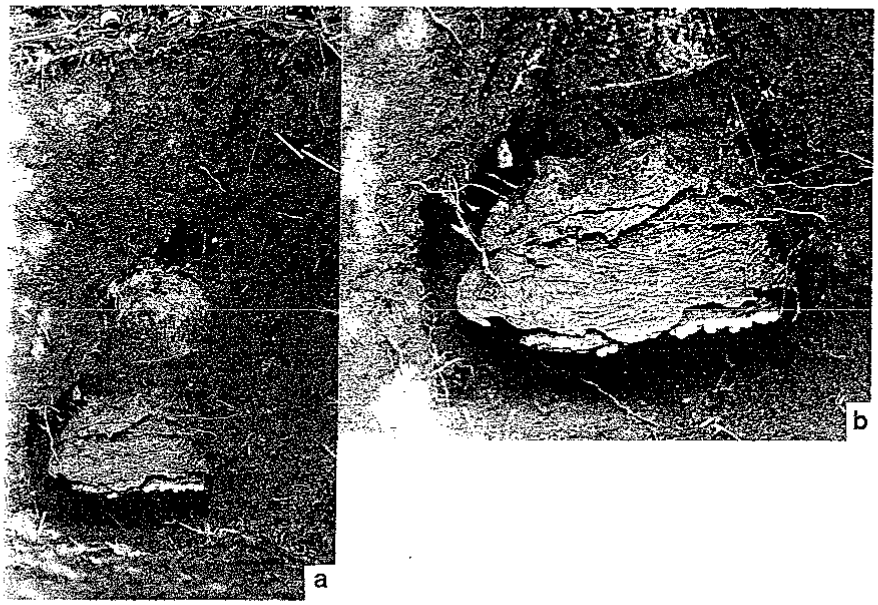

Fig. 1. a. Nest of *Vespa philippinensis* in a hillside. Soil has been removed to reveal the entrance tunnel (indicated by an arrow), cavity and intact nest. —— b. Closer view of the same.

The envelope (Fig. 2) was roughly laminar, about 2–4 layers thick in most places. Twenty haphazard measurements of the space between these layers gave values of 9–20 mm, with a mean of 13 mm, about the right separation to allow a worker to walk within the envelope. The layers were not discrete over large areas, though. They were connected by pillars which tended to become partitions, and there was frequent anastomosing of the layers. We might view this as intermediate between a strictly laminar and a cellular arrangement. It does not resemble the imbricate envelope of *V. affinis* and *luctuosa*, among others. The envelope covered

Fig. 2. Detail of *V. philippinensis* nest-envelope.

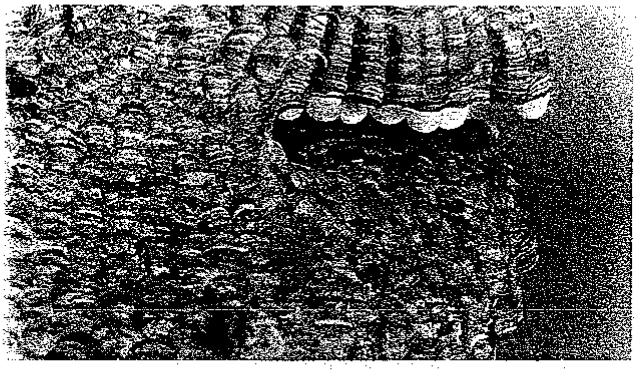

Fig. 3. *V. philippinensis* comb which has curled around to occupy two different levels.

the sides and top of the nest, leaving the combs exposed below (Fig. 1b).

The nest had four combs with 1,560 cells and a face-area of about 1,450 cm^2. Comb 1 curved sideways in a rather tight arc, with one end at a lower level than the other. Comb 2 lay below the higher part of comb 1 and on about the same level as the lower part. Comb 3 was at about the same level and had about a 5 cm line of fusion with the low end of comb 1. Comb 4 was below these and did not fuse with any of them. Like comb 1, it was in a split-level arc, and in this case one end of the arc lay below the other, as if they were two separate combs (Fig. 3). Despite this irregularity, the tops of combs were relatively flat and smooth (Fig. 4), not roughened by building cell-bases.

The distance between the top of one comb and the next was about 35–55 mm. Cells were also quite variable in length and in the degree to which cocoons extended outside of the walls. Cocoons commonly protruded 10 mm or more beyond the cells mouths (Fig. 5), some as much as 20 mm, while some protruded not at all. Given these sources of unevenness, it is not realistic to speak of a specific "wasp

Fig. 4. Detail of *V. philippinensis* comb-top.

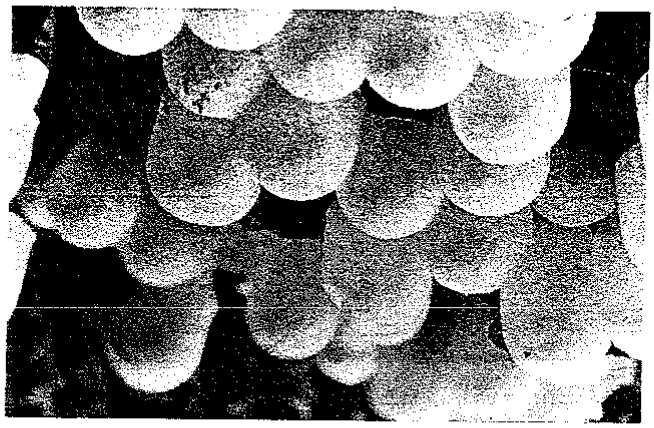

Fig. 5. *V. phillipinensis* cocoons protruding from their cells.

space".

Cells fell into two size-groups with mean diameters of 9.4 mm (range 8.6–10.0) and 11.1 mm (range 10.4–11.7). Combs 1 and 2 were entirely of small cells, comb 3 was of small cells except at the two ends, and comb 4 was entirely of large cells.

Checking every 10th cell, we estimated that 1,480 cells had been utilized to rear new wasps. Dissection of a smaller sample of cells showed no reutilization of cells in any comb.

3. *V. affinis*

The two hornet species of Palawan, *V. tropica* and *affinis*, are both abundant, and nests of *V. affinis* are not difficult to locate. The following description is based on the dissection of nine nests and the less complete examination of eleven others from Palawan and associated smaller islands, mostly in the Aborlan area.

All nests were in trees and bushes, and we have not heard any report of *V. affinis* nesting in a different situation in the Philippines. Heights varied from less than 1 m above the ground to an estimated 16 m, with most at about 2–3 m. In some cases the nest substrate was a single tree branch, but other nests were in fairly dense vegetation, with several small branches or twigs running through them. When the nest was based on slender, flexible vegetation it might be subject to considerable movement by wind. In particular, one exceptionally large nest based on some vines swayed like a ripe fruit on windy days.

As illustrated in Fig. 6, mature nests are roughly pear-shaped, broadening from the top to the rather abruptly truncate base. The entrance hole is usually round in early nests, but lengthens into a vertical oval in many later nests, often twice as long as wide. The envelope is of moderately fine carton (Fig. 7 a) with an imbricate gross structure, *i.e.*, laid down in overlapping dishlike sections (Fig. 7 b).

One of the nests had two large holes on the basal edge and six smaller holes in

Fig. 6. *Vespa affinis* nests. —— a–b. Two mature nests intact. —— c–d. The same nests with the envelope cut away.

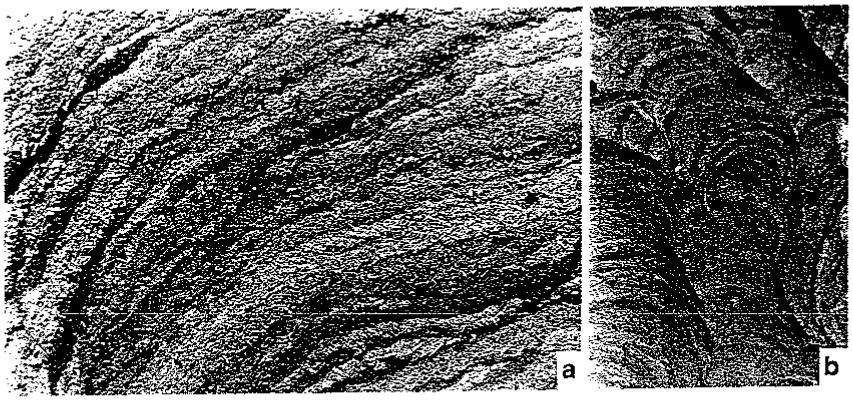

Fig. 7. Details of *V. affinis* nest-envelope. —— a. Fine structure of the carton. —— b. Larger view, showing imbrication.

the walls. Wasps were entering and leaving through all of these, though only the two larger ones had the appearance of regularly fashioned entrance holes, the others looking more like a result of damage.

The most striking oddity of the nest is the hypertrophy of the envelope above the combs into a prominent *roof-cone* (Fig. 6 c-d) which contributes substantially to the nest's total height (Table 1). This has a cellular structure (Fig. 8) somewhat like the nests of many nasute-termites. Unlike the roof area in the examined *V. philippinensis*, the roof-cone of *V. affinis* is not provided with passageways, and we have seen no indication that wasps commonly penetrate it.

It is very likely that the nests of *V. affinis* commonly reach larger sizes than those of any other Philippine hornet. Of those which we have examined closely, one of the largest had nine combs with more than 12,000 cells and a total comb-face area of about 0.8 m^2 (Fig. 9). With a total height of 96 cm, including the large roof-cone, and a width near the base of about 63 cm, its total volume was roughly 140 liters. The largest nest seen had a height of about 1.1–1.4 m and a basal width of 0.9–1.1 m, and its volume must have been around three times as much. Mature *V. affinis* nests of more than 50 liters are evidently fairly common in Palawan.

The later (lower) combs tend to reach greater size than earlier ones (Figs. 6,

Table 1. Dimensions of five large *V. affinis* nest from Aborlan, Palawan.

Number of combs	Mean diameter at base	Height of roof-cone	Height of nest below roof-cone
7	33 cm	7 cm	26 cm
7	32	28	36
9	63	57	39
10	43	28	36
13		10	40

Fig. 8. Cross-section of *V. affinis* roof-cone to show its cellular structure.

9). Together with the roof-cone, this accounts for the overall pear-shape of the nest. Combs are regular in their horizontal flatness and discreteness from each other. None of the nests examined showed any split-level combs or fusing between them. Nonetheless, the space between combs is quite variable, between about 12–25 mm. Large combs were invariably connected by numerous petioles, though in many cases one stout central petiole stood out from the auxiliaries.

Fig. 9. Total combs (numbered in sequence) of a mature *V. affinis* nest, spread out face-up.

Table 2. Mean cell diameters from the last several combs in three *V. affinis* nests from Aborlan, Palawan. In about half of the combs, two different cell samples were measured. All figures in millimeters.

	Comb 5	Comb 6	Comb 7	Comb 8	Comb 9	Comb 10	Comb 11	Comb 12	Comb 13
Nest A	9.7	8.0	8.2	—	—	—	—	—	—
Nest B		8.0	7.9	8.1	9.2	8.9, 9.0	—	—	—
Nest C	7.7	8.1	7.7	8.5, 8.7	8.4, 9.4	7.5, 8.7	8.9, 9.4	8.9, 9.2	7.8, 8.2

Petioles were often flattened in the horizontal plane, and some even formed elongate ribbons. They appeared to be of a crude, dust-like carton.

The cells of *V. affinis* do not fall into two clear size-types, nor could we readily distinguish small-cell and large-cell combs. Measurements from three nests (Table 2) show only a very rough bimodality of cell-diameters, with vague peaks at about 8.0 and 9.0 mm. Furthermore, the distribution of cells of different sizes among the combs appears chaotic. Unfortunately we do not have measurements from earlier combs of these nests, which might have clarified the pattern.

We examined only one nest closely for cell reutilization, sampling cells from each of the 13 combs. A large proportion of cells in the first six combs had reared wasps, as evidenced by fecal pellets in the bases, but in each of the remaining combs we found few or no fecal pellets. Of 100 sampled cells which had reared wasps, only five had been reutilized to rear a second brood and one to rear a third. A second line of evidence for the disuse of cells after eclosion was the closure with carton of cells in the upper combs of large nests (Fig. 10). In the nest just mentioned, combs 1–3 and 7 were mostly papered over in this manner, combs 4–6 and 8 had many cells papered, combs 9 and 10 had only a few papered, and only the last three combs still had all cells open for business. In other large nests we found at least the first comb mostly papered over.

It is not known how long abandoned nests retain their structure if left in

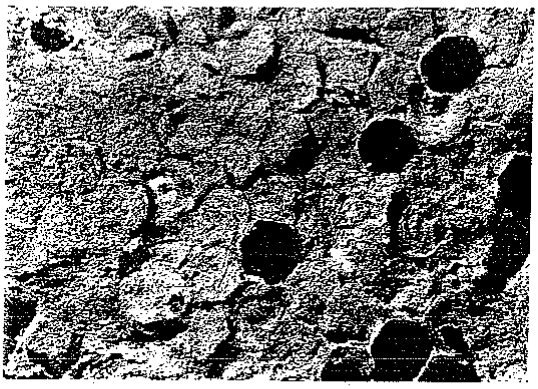

Fig. 10. Part of an upper comb of *V. affinis* nest, showing papered-over cells.

Fig. 11. Detail of *V. luctuosa* nest-envelope, showing imbrication.

place, but they evidently do not decay very rapidly. Some nests which had reportedly been vacant for several weeks when collected were still largely intact. Aside from various solitary insects, these had rodents, social wasps (*Ropalidia* sp.) and three colonies of ants nesting in them. These animals appeared simply to utilize the sheltered space within the envelope, without particular reference to the cells.

4. *Vespa luctuosa*

We dissected 13 *V. luctuosa* nests of varying states of maturity and saw about 13 others in place. About 2/3 of these were on Luzon, in the provinces of Batangas, Laguna, Camarines Sur and Sorsogon, the rest on Samar and Leyte.

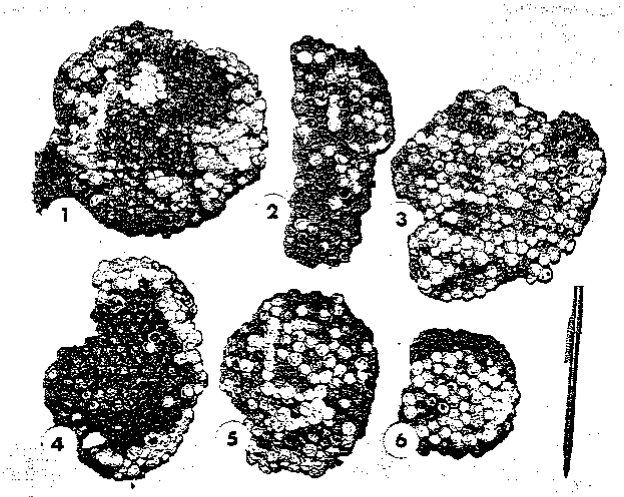

Fig. 12. Total combs (numbered in sequence) of a mature *V. luctuosa* nest, spread out face-up.

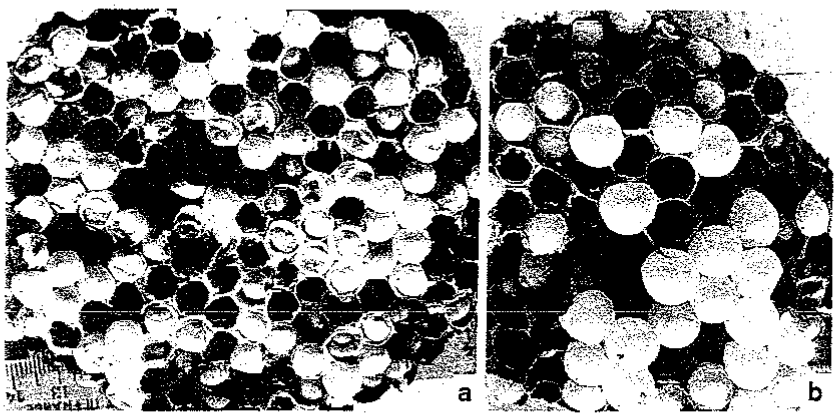

Fig. 13. Details of (a) small-cell and (b) large-cell combs of *V. luctuosa*, to the same scale.

For present purposes we will not maintain a distinction between *V. l. luctuosa* of Luzon and *V. luctuosa luzonensis* [sic] of the Visayas islands, including Samar and Leyte.

One of the 26 nests seen was in the ceiling of an abandoned house, largely without walls, in Batangas province. This nest failed at an early stage, and we have not seen or heard of other *V. luctuosa* nesting on buildings. All others were in vegetation from less than 1 m to about 6 m above ground. Most were in bushes or small trees, with several small branches going through them, and only a few were in larger trees and based on a single branch.

Small nests are approximately spherical, but as the nest grows it elongates vertically. The envelope is much like that of *V. affinis* and similarly imbricate (Fig. 11), with complete closure below. The outstanding difference is in the absence of a roof-cone in *V. luctuosa*. The roof is not strikingly thicker than the walls or

Table 3. Cell-reutilization in combs 1, 2 and 4 of two six-combed *V. luctuosa* nests. Each figure is based on a haphazard sample of 30 cells from various parts of the comb, each cell having at least one fecal pellet.

	Number of fecal pellets per cell					
	1	2	3	4	5	6
			Comb 1			
Nest A	7	13	10	0	0	0
Nest B	1	5	5	10	9	0
			Comb 2			
Nest A	13	17	0	0	0	0
Nest B	4	18	7	1	0	0
			Comb 4			
Nest A	30	0	0	0	0	0
Nest B	14	16	0	0	0	0

floor. In one mature nest the envelope divided into two fairly distinct layers, each comprising a complex of imbricate carton, separated by a space which was about right for walking workers. The entrance hole is an undistinguished circle or oval in the envelope wall.

The largest nest dissected had six combs with an estimated 1,252 cells and a face-area of about 912 cm^2 (Fig. 12). The largest nest seen appeared to be roughly twice this size. In all nests we found the combs to be discrete, without split levels or fusion. Of the multiple petioles connecting adjacent combs, one central one was usually distinctly larger. In large nests the domed comb tops were generally daubed with additional carton which obscured the outlines of the cell bases. Such *plastering* was quite distinct from the more structured sheets of carton making up the cells and instead resembled that laid down on the expanding petioles. Of the few petioles which we dissected, some showed signs of early varnishing underneath the plastering.

Measurements from four nests show two easily recognized size-classes of cells (Fig. 13). The modal diameter of large cells is 9.9–10.0 mm in each case, but small cells are less consistent among these nests, with modes between 6.8–7.9 mm. In each nest the first comb was of small cells and the other two to five combs of large cells. One nest showed a very few peripheral large cells in comb 1, and two others had a very few small cells within comb 2. In no case would we characterize any comb as mixed or transitional.

In each of two six-combed nests we counted fecal pellets in sample cells of combs 1, 2 and 4. As seen in Table 3, cell-reutilization was the rule in combs 1 and 2, with some cells of comb 1 rearing as many as five wasps in one of the nests. As expected, there is a clear trend of fewer brood-cycles in later combs. At the same time, it is evident that early combs can become disused before the end of the colony-cycle. In each of these two large nests, the cell walls in the main part of comb 1 had been removed (Fig. 14) and much of what remained was papered over. To a

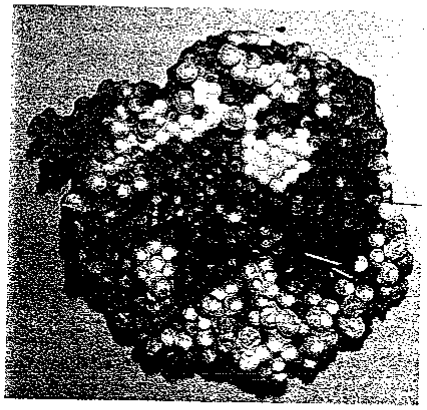

Fig. 14. Comb 1 of a mature *V. luctuosa* nest, showing excavated central part.

decreasing degree, subsequent combs showed similar excavation and/or papering.

Discussion

The present literature on the nests of hornets includes some information on more than half of the species. We have summarized this in Tables 4 and 5 in order to show what is known, to facilitate comparative studies, and as a suggested checklist of data to be recorded in future studies.

Nests of *V. affinis* and *V. tropica* in the Philippines show good agreement in site and structure with conspecific nests elsewhere in East Asia. The endemic *V. philippinensis* has a nest much like *V. tropica*, though the only colony described to date (STARR, 1987) was much larger than any recorded from *V. tropica*.

Our results from two below-ground and two above-ground nesting species represent a start in understanding which major features of nest structure are largely set by the species-characteristic nest-site and which are independent of nest-site. Both in the Philippines and elsewhere, the form of the envelope shows some good correlation with nest-site. Present indications are that species which characteristically nest below ground build laminar envelopes and those which nest in exposed situations above ground consistently have imbricate envelopes.

On the other hand, it is puzzling that the strength of the roof-cone differs so much among species building exposed nests in the humid tropics. It makes good adaptive sense that tropical *V. affinis* (and apparently *V. analis*) should consistently build a roof-cone as a protection against rain (VECHT, 1957), but why does *V. luctuosa* in apparently identical situations not have one? It remains to be investigated whether *V. luctuosa* has a superior paper technology which renders a massive roof-cone unnecessary.

The proximal cause of the large roof cone in *V. affinis* and its absence in *V. luctuosa* probably has to do with differences in their treatment of early combs. Note that in *V. affinis* these are hardly at all reutilized for successive cycles of brood, while *V. luctuosa* has the highest reutilization tendency recorded (Table 5). Coupled with this is the tendency of *V. affinis* to paper over early combs and to fill and seal the upper area as it is abandoned. This alone can result in a substantial roof-cone in a large nest, regardless of whether there is any special deposition of pulp on the outside above. The papering over of old cells is known from several *Vespula* spp. (EDWARDS, 1980) and is seen to a slight degree in *Vespa analis* (YAMANE & MAKINO, 1977), but our results from *V. affinis* are apparently the first report of any *Vespa* papering over large area of comb-face.

The nests of *V. luctuosa* differ most strikingly from those of all other Philippine species, as well as most *Vespa* spp. elsewhere, in the large, clear distinction between small and large cells. This is consistent with the observation of an exceptionally sharp physical separation between queens and workers (KOJIMA, 1982; pers. obs.) and suggests a somewhat higher level of social complexity. The relative

Table 4. Nest sites of *Vespa* spp. A single + indicates that the species has been recorded nesting in such a site. A double + indicates the characteristic nest site, if known.

Species	Locality	Nest sites				Reference
		Below-ground cavity	Above-ground cavity	Trees and shrubs	Exposed on buildings	
affinis	Taiwan			+	+	Matsuura, 1973; pers. obs. (CKS, RSJ)
affinis	Palawan			+		this paper
affinis	Thailand and Malaya			+		Vecht, 1957; Seeley & Seeley, 1980
analis	Japan			+	+	Matsuura, 1971 a–b, 1974; Yamane & Makino, 1977
analis	Taiwan and Java			+		Matsuura, 1973; Vecht, 1957
basalis	Taiwan			+		Matsuura, 1973; pers. obs. (RSJ)
crabro	Japan	+	+			Matsuura, 1971 a–b, 1984
crabro	Europe	+	+		+	Saussure, 1853–1858; Janet, 1903; Guiglia, 1948; Spradbery, 1973; Edwards, 1980
crabro	USA		+		+	Duncan, 1939; pers. obs. (RSJ)
dybowskii	Japan		+			Sakagami & Fukushima, 1957
luctuosa	Luzon, Samar and Leyte			+		Williams, 1919; Kojima & Yamane, 1980; this paper
mandarinia	Japan	+	+			Matsuura, 1971, 1984; Matsuura & Sakagami, 1973; Yamane & Makino, 1977
orientalis	Europe	+	+			Guiglia, 1948;
orientalis	Israel	+	+			Ishay *et al.*, 1967
philippinensis	Leyte	+				this paper
simillima	Japan	+	+	+	+	Matsuura, 1971, 1984; Yamane, 1974
tropica	Japan	+	+			Matsuura, 1971, 1984
tropica	Luzon	+				this paper
tropica	Malaya	+	+			Pagden, 1952; Vecht, 1957
tropica	India		+			A. S. Joshi, pers. comm.
velutina	Taiwan	+		+		Matsuura, 1973; pers. obs. (CKS, RSJ)
velutina	Java			+		Vecht, 1957

Table 5. Features of mature nests of *Vespa* spp. An imbricate envelope is one composed of overlapping dish-like sections, each outwardly convex, while in a tubular-imbricate envelope the sections are vertically elongate. A laminar envelope consist of broad, largely distinct sheets. Plastering is the daubing of pulp onto a surface.

Species (locality)	Envelope: Structure	Envelope: Roof-cone	Envelope: Closed at bottom	Combs: Maximum combs recorded	Combs: Shape of top	Combs: Plastering of top	Combs: Auxiliary petioles	Combs: Maximum cells recorded	Combs: Cell types	Cells: Mean or modal diameter (mm)	Cells: Reutilization	References
affinis (Taiwan)	imbricate	–	+	5	flat	+	+	6178		small: 7.2 large: 9.0		Matsuura, 1973; pers. obs.
affinis (Palawan)	imbricate	+	+	13	flat	–	+	14000	uncertain	very variable	very little	this paper
affinis (Thailand)	imbricate, plastered	moderate	+	7				9600				Seeley & Seeley, 1980
affinis (Malaya)	imbricate, plastered	+	+									Vecht, 1957
analis (Korea)										small: 8.0		pers. obs.
analis (Japan)	imbricate	–	+	4	domed or conical		–	441	1: small 2: mixed others: large	small: 8.2 large: 9.0	very little	Yamane & Makino, 1977; Matsuura, 1984; pers. obs.
analis (Taiwan)	imbricate	–	+	4				747		range: 8.7–9.5		Matsuura, 1973
analis (Java)	imbricate	+	+	9								Vecht, 1957
basalis (Taiwan)	mostly laminar	–	+	5	flat			>2300		small: 7.5		Matsuura, 1973; pers. obs.
crabro (Japan)	tubular imbricate			7	flat					range: 7.3–9.0	≤3 broods in early combs	Matsuura, 1983
crabro (W. Europe)	tubular imbricate		±	12						comb 1: 7.4	small-cell combs only	Janet, 1903; Guiglia, 1972; Spradbery, 1973; Edwards, 1980
crabro (USA)	tubular	–	±	16	flat			3528	1: small 2 or later: mixed others: large	small: 8.4 large: 10.9		Beutenmuller, 1898; pers. obs.

dybowskii (Japan)				3				683	1: small 2: mixed 3: large			Sakagami & Fukushima, 1957
luctuosa (Luzon, Visayas)	imbricate	–	+	6	domed	+	+	1252	1: small others: large	small: 7.4 large: 10.0	≤5 broods in early combs	Kojima & Yamane, 1980; this paper
mandarinia (Japan)		–	incomplete	7	conical		+	4661	1–2: mixed others: large	small: 10.6 large: 13.6	≤3 broods in combs 1–2	Matsuura, 1971a, 1984; Matsuura & Sakagami, 1973; Yamane & Makino, 1977; pers. obs.
orientalis (Israel)	prob. laminar							1847		small: 8.0		Ishay *et al.*, 1967; pers. obs.
philippinensis (Leyte)	mostly laminar	–	–	4	slightly domed	–	few	1560	1–2: small 3: mixed 4: large	small: 9.4 large: 11.1	very little	this paper
simillima (Japan)	imbricate	–	+	10	flat		+	14000		small: 7.6 large: 9.5	≤3 broods in early combs	Iwata, 1971; Yamane, 1974; Matsuura, 1984; pers. obs.
tropica (Japan)	laminar			3	domed or conical					comb 1: 10.0 comb 2: 10.5	≤3 broods in early combs	Matsuura, 1971a, 1984; Matsuura & Sakagami, 1973; pers. obs.
tropica (Luzon)	mostly laminar	–		4 (immature)	domed or conical	–		450 (immature)		variable		this paper
tropica (India)	laminar			3	slightly domed	–						photographs by A. S. Joshi
velutina (Taiwan)	mostly laminar	–	+	6				568 (prob. immature)		comb 1: 7.4 comb 4: 9.0		Matsuura, 1973; pers. obs.

distinctiveness of small and large cells and their distribution among the combs are perhaps the most important questions at present in the comparative study of vespine nest structure. We would very much like to see these data become a central part of any description of mature nests.

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