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BIONOMICS OF VESPA ANALIS INSULARIS AND V. MANDARINIA LATILINEATA IN HOKKAIDO, NORTHERN JAPAN, WITH NOTES ON VESPINE EMBRYO NESTS (HYMENOPTERA: VESPIDAE)

By SEIKI YAMANE and SHUN'ICHI MAKINO

Abstract

YAMANE, SK. and MAKINO, S. 1977. Bionomics of *Vespa analis insularis* and *V. mandarinia latilineata* in Hokkaidô, northern Japan, with notes on vespine embryo nests (Hymenoptera: Vespidae). Ins. matsum. n.s. 12: 33 pp., 4 tabs., 43 figs. (35 text-figs., 2 pls.).

Bionomics of *Vespa analis insularis* and *V. mandarinia latilineata* in Hokkaidô is given. Early colonial development in *V. analis insularis* was observed for the construction rates of the cells and envelope, change in nest shape, and behaviour and activity of the foundress. Contents and size of some mature nests of *V. analis insularis* and *V. mandarinia latilineata* were examined and compared with those studied in southern Honshû. The total production of colonies was estimated based upon both mature and dissolved nests. The results show that the productivity of nests in Hokkaidô is slightly less than that of nests in southern Honshû. The mature nest structure of both the species is described, and the size difference of cells among different combs is figured and explained. The embryo nests of some vespine genera are described. The roles of envelope and some taxonomically important characters of the embryo nest are discussed along the line of reasoning advanced by R. L. Jeanne.

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Contents

Introduction 3
1. Nests examined or observed 3
2. Habitat and nest site 3
3. Colonial development
  3.1. Early colonial development 4
  3.2. Change in nest shape in early stage 6
  3.3. Behaviour of the foundress
    3.3.1. Nest construction 7
    3.3.2. Nest defence 7
    3.3.3. Resting 7
    3.3.4. Other intranidal activities 8
    3.3.5. Daily activity 9
    3.3.6. Extranidal activities during first 40 days 10
  3.4. Mature nest and productivity
    3.4.1. Nest contents 11
    3.4.2. Productivity 11
4. Mature nest structure
  4.1. Description of nest
    4.1.1. *V. analis insularis* 17
    4.1.2. *V. mandarinia latilineata* 20
  4.2. Cell size 21
5. Notes on vespine embryo nests 21
  5.1. Description
    5.1.1. Genus *Vespa* 22
    5.1.2. Genus *Vespula* 22
    5.1.3. Genus *Dolichovespula* 22
  5.2. Roles of envelope 23
  5.3. Some characters of taxonomic importance 25
  5.4. Conclusion on embryo nest 26
Acknowledgements 26
References 27
Plates 29

Introduction

Four species of the genus *Vespa* have reliably been recorded from Hokkaidô (S. Yamane, 1970). Of these *V. simillima* Smith and *V. crabro flavofasciata* Cameron, both essentially inhabitants of the temperate zone, are commonly and widely distributed in Hokkaidô, while *V. analis insularis* Dalla Torre and *V. mandarinia latilineata* Cameron, which are geographical races of basically warm temperate to subtropical or tropical species, are rather localized in northern Japan. Bionomic studies of the latter two forms in Hokkaidô may give interesting information concerning differences in life mode between them and temperate inhabitants (*V. simillima*, *V. crabro*, *Vespula* and *Dolichovespula*), and between them and southern conspecific populations.

In this paper data are given concerning bionomics of *Vespa analis insularis* and *V. mandarinia latilineata* mainly based upon observations in Sapporo, Hokkaidô. In preparing a description of the embryo nest of *V. analis insularis* we have felt the need to review studies of vespine embryo nests. Though our knowledge in this respect remains still very incomplete, we will give a brief review of vespine embryo nests and biological interpretations for some important characters.

1. Nests examined or observed

Nests dealt with in this paper are listed in Table 1. Collected nests were examined for the number of adults and immatures, total number of wasps emerged and size of nests and combs. Total production was estimated by the methods developed by S. and Sk. Yamane (1975). Some mature nests were used to describe the structure and to measure the cell size of different stories or zones in the nest. Two young nests of *V. analis insularis* (A7612 and A7615) were continuously observed to study the early colonial development and foundress behaviour. Sections *3.1.* to *3.3.* will not refer to *V. mandarinia latilineata*, because of our failure to observe its embryo nest.

2. Habitat and nest site

Vespa analis insularis and *V. mandarinia latilineata* are generally not common in Hokkaidô, and seem to be distributed only in southern parts. The known localities for them are as follows:

V. analis insularis: Chikabetsu, Tokachi County; Yûbari, Sorachi County; Sapporo and Jôzankei, Ishikari County; Shiraoi, Iburi County; Ônuma[1], Kameda[1] and Hakodate,[2] Oshima County.

V. mandarinia latilineata: Tsukigata[3] and Yûbari, Sorachi County; Teine, Sapporo and Jôzankei, Ishikari County; Ônuma,[1] Oshima County.

Both the forms live mainly in low mountains, parks and forests, but are rare or absent in plains and high altitudes.

V. analis insularis exclusively builds nests on trees or in bushes (Figs. 36–42) as reported by Matsuura (1971a) for populations of southern Honshû. They are usually suspended from twigs (3–6 mm in diameter) within 2 m above the

1) Munakata and S. Yamane, 1970. 2) Smith, 1856 (referred to as *Vespa Japonica* Smith). 3) van der Vecht, 1959.

Table 1. Sizes and populations of nests of *Vespa analis insularis* and *V. mandarinia latilineata* dealt with in this paper.

Nest no.[1]	Date and locality[2]	No. of adults					Nest diameter in cm.
		f♀	♂	♂	n♀	Total	
A7102	Aug. 16, 1971. BGHU						
A7203	Oct. 1972. Maruyama						15.0
A7304	Oct. 5, 1973. Maruyama						
A7408	Jul. 12, 1974. Okushiri Isl.	1					
A7409	Sep. 7, 1974. BGHU		7	33		40	14.0×15.0
A7410	Sep. 17, 1974. Azabu		20	5		25	11.5×12.0
A7511	Sep. 4, 1975. BGHU		24	22	48	94	
A7612[3]	, 1976. Maruyama						
A7613	May 30, 1976. Maruyama						
A7614	May 30, 1976. Maruyama	1					
A7615[3]	, 1976. Maruyama						
A7616	May 30, 1976. Maruyama	1					
A7617	Jul. 19, 1976. GHU	1	6				7.5× 7.0
A7618	Aug. 21, 1976. BGHU	1	29	6		36	13.5×16.0
A7619	Aug. 21, 1976. BGHU	1	35	16		52	13.0×17.0
A7620	Aug. 21, 1976. BGHU						
A7621	Sep. 13, 1976. BGHU		12	56			15.0×18.5
A7622	Oct. 1, 1976. BGHU						14.5×18.0
A7623	Oct. 8, 1976. BGHU						12.5×16.5
Mn7301	Aug. 26, 1973. Maruyama	1	110			111	
Mn7602	Sep. 15, 1976. BGHU	1	184	24	3	212	

1) "A" and "Mn" stand for *V. analis insularis* and *V. mandarinia latilineata*, respectively.
2) All in Sapporo, Hokkaidô, except for A7408 (BGHU, Botanical Gardens of Hokkaidô University; GHU, Grounds of Hokkaidô University).
3) Nest continuously observed by us.

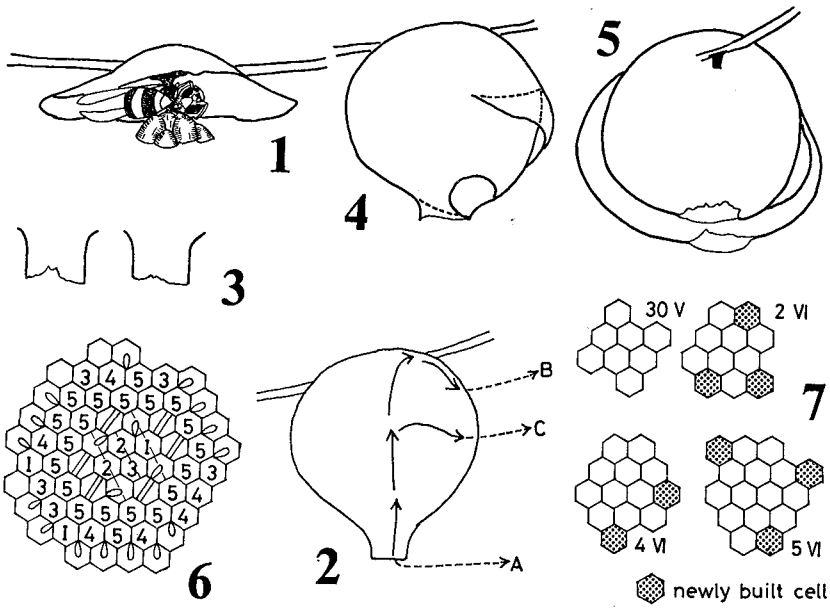
ground, and most of the nests collected in Sapporo (14 out of 17 nests collected) were within 1 m above the ground. We have observed only three nests of *V. mandarinia latilineata* in Sapporo, of which two were built above ground in hollow trees and one underground (the last without further information).

3. Colonial development

3.1. Early colonial development

Concerning the early development of the colony in *V. analis insularis* only a small amount of data are available. Nest A7612 was observed from its initiation. In the first ten days or so the mean number of cells constructed per day was 1.6, closely agreeing with that in other temperate social vespids (cf. Brian and Brian, 1948; Yoshikawa, 1962) (Fig. 8). After the envelope covered the nest comb, it was difficult to count cells. Extranidal activities of workers were first observed on July 7. The number of worker trips rapidly increased until July 10, but thereafter fluctuated around 15 per hour (Fig. 10C). The nest was destroyed by an accident on July 30; at that time the first comb was composed of 107 cells and the second one was about to be built. The total number of workers emerged was estimated at 32, and ten central cells of the first comb were occupied by second generation prepupae or pupae.

An embryo nest (A7408) collected on July 12, 1974 on Okushiri Island had a



Figs. 1–7. Embryo and young nests of *Vespa analis insularis*. 1. Initial nest with a foundress resting around the pedicel (A7612: May 30, 1976); 2. Typical courses of the inspecting walk by the foundress on the embryo nest envelope (A: Direct departure; B, C: Departure preceded by a long and short inspection walk); 3. Entrance projection (vestibule) of embryo nest, showing ragged ventral edge; 4. Young nest after worker emergence, showing a new entrance and second envelope sheet (A7615; Jul. 14, 1976); 5. Young nest with plural envelope sheets (A7617: Jul. 19, 1976, T. Sunose leg.). Sectional view, comb removed; 6. Cell map of the first comb of Nest A7617 (Symbols, see Fig. 12); 7. Progress of cell construction in Nest A7612.

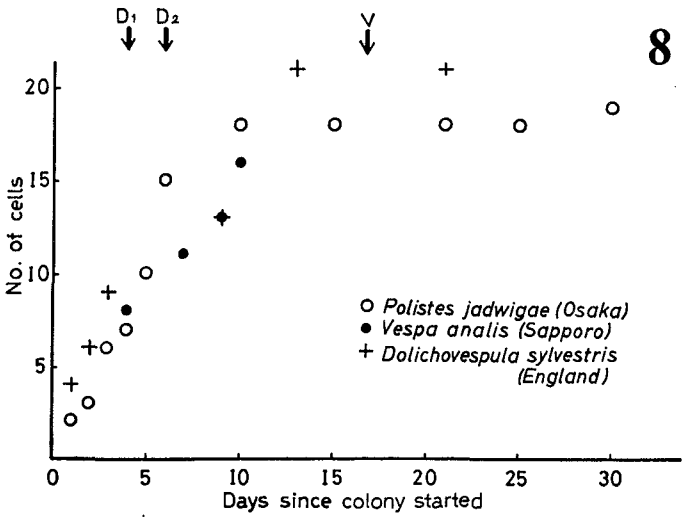


Fig. 8. Rate of envelope and cell construction in some temperate social vespids (*P. jadwigae*: Yoshikawa, 1962; *D. sylvestris*: Brian and Brian, 1948; *V. analis insularis*: original; D_1, D_2 & V, see text).

founding queen, a completed envelope and a small comb comprising 21 cells with two 5th instar larvae, eight young larvae and four eggs (Fig. 13). A young nest (A7617) collected on July 19, 1976 in Sapporo had a foundress and six workers, and a comb comprising 65 cells. In this nest eight workers had emerged and cells for the second use were occupied by young larvae or eggs (Fig. 6).

The first sheet of envelope was completed on or about the 17th day from the nest initiation in Nest A7612 (Fig. 8, V). On the other hand, according to Brian and Brian (1948) a founding queen of *Dolichovespula sylvestris* Scopoli completed the first sheet on the 4th day (Fig. 8, D_1), the second on the 6th day (D_2), and another queen completed the first sheet on the 3rd day, the second on the 4th day, the third on the 6th day and the fourth on the 7th day. Potter (1965; after Spradbery, 1973) also shows that after about three days a queen of *Vespula vulgaris* Linné will have completed its first sheet. The construction rate of the envelope in *V. analis insularis* can be said to be very slow in comparison with that in the other vespine genera.

3.2. Change in nest shape in early stage

The following description is mainly based upon observations on Nest A7612, A7615 and A7617. Although the very initiation of a nest by the foundress has not been observed by us, the first step of nest construction by female *Vespa* wasps is, according to Matsuura (1971), to make a pedicel for the support of a small comb. Thereafter the envelope was constructed in parallel with the comb construction (Figs. 1, 38), and it took about 17 days to complete the first sheet in Nest A7612. The completed envelope in the embryo nest is flask-shaped, being composed of spherical and cylindrical parts. It varied somewhat in shape and size as mentioned by Matsuura (1971). In four nests found in Sapporo in 1976 the cylindrical part (=vestibule) measured 13 to 23 mm in length, with the lower edge ragged (Fig. 3); it is distinctly shorter than that figured by Matsuura for populations of southern Honshû. Some examples are shown in Figs. 36, 37 and 39, and Table 2. Flask-shaped nests always contained a foundress alone, and even if workers had already emerged they probably did not go out of the nest at this stage. After workers began foraging they closed the original entrance and made a

Table 2. Dimensions of completed embryo nests of *V. analis insularis* from Sapporo and Honshû.

Nest no.	Diameter of spherical part (mm)	Total length (mm) [A]	Vestibule length (mm) [B]	B/A
A7612	68	90	23	0.26
A7614	64	78	13	0.17
A7615		80	16	0.20
A7616	66	80	16	0.20
[A7224]				0.34
[A7625] from Niigata	73	114	34	0.30
Nests from Wakayama	61-74[1] (n=21)			0.38-0.50[2] (n=3)

1) Cited from Matsuura (1971b).
2) Measurements based on some photographs in Matsuura (1971b; 1976).

new one near it (Fig. 4). Then they began constructing the second sheet from the upper portion of the first sheet. It was usually composed of irregularly arranged "shells" (Figs. 5, 40).

3.3. Behaviour of the foundress

3.3.1. Nest construction. On returning to the nest with a load of pulp the foundress directly entered the nest and chewed the pulp on the comb, while always rubbing the hind legs together. The time spent in chewing the pulp ranged from 17 to 58 seconds (m=39.5, n=15). In the case of envelope construction, she then clung to the edge of the envelope under construction and searched for a suitable part to be enlarged. She then slowly walked backwards while she put the material on with her mandibles and fore legs, followed by repeated forward-backward walkings in order to thin the material, as reported by Brian and Brian (1948) for *Dolichovespula sylvestris*. The time spent in applying-and-thinning the material varied from 87 to 210 seconds (m=150.1, n=15). Envelope construction was observed throughout the daytime except for early morning (Fig. 9C). Detailed observations were not made on cell construction, which involved cell initiation and the elongation of cell walls. The foundress always began cell construction with chewing the pulp on the comb as seen in envelope construction. Time spent was 130 and 210 seconds (m=170, n=2) in the cell initiation and 146 to 245 seconds (m=207.1, n=8) in the elongation of cell walls. These operations were observed at various time of the day (Fig. 9C; C, CI). An additional treatment of the pulp previously applied was often observed for both envelope and cell walls. This operation was begun at 20 to 55 seconds (m=33.7, n=6) after the first treatment was finished, when the concerned part was not completely dried. It was composed of the thinning operation with forward-backward walkings, taking 20 to 83 seconds (m=40, n=6). Furthermore, a third treatment was sometimes observed even 30 minutes after the first treatment was finished.

3.3.2. Nest defence. Two actions probably related to defence behaviour were performed by the *V. analis insularis* foundress during the solitary stage. When we gave physical stimuli to the nest, for example by tapping on the envelope, the foundress rushed out from the nest with rustles, and violently walked about on the envelope. This behaviour seems somewhat different from that seen in the *Dolichovespula* foundress, which rushes out from the nest and flies about it, or even suddenly falls to the ground.

The other supposed defence action shown by *V. analis insularis* foundress was to inspect the envelope surface, especially at the attachment point of the nest to the twig. On one occasion (June 25) the foundress found a spider approaching the nest, and then she captured and dumped it, and flew back to the nest. Every foraging sortie observed for about 2.5 hours after this incident was preceded by a walk over the envelope surface with antennae directed forwards. The time spent in this inspecting walk gradually decreased as time went on, that is, 16, 13, 12, 9, 9 and 11 seconds (m=11.7). Some typical courses of the walk are shown in Fig. 2. This action sometimes occurred in the absence of any noticeable stimuli to the nest. Even in these cases an inspection preceded several foraging flights.

3.3.3. Resting. The resting posture of the foundress observed in *V. analis insularis* is as seen in *Dolichovespula sylvestris* and *Vespa crabro* (Brian and Brian, 1948; Spradbery, 1973). (Our unpublished data suggest that this posture may be

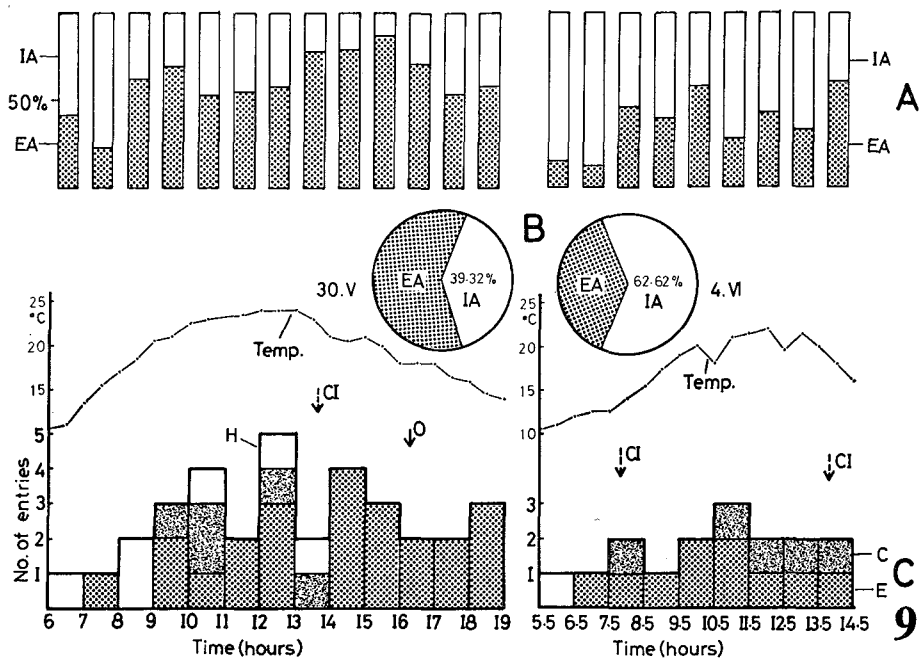


Fig. 9. Daily activity of the foundress of *Vespa analis insularis* (A7612). Left: May 30, 1976; Right: June 4, 1976. A. Intra-(IA) and extranidal (EA) activities in each hour in percentage; C. Number of entries per hour (C: with pulp for cell construction; E: with pulp for envelope construction; H: with honey or none; CI: cell initiation; O: oviposition).

general through *Dolichovespula* species except for labour-parasitic ones.) The foundress when resting curled horizontally around the pedicel (Fig. 1). We have not observed the foundress resting on the comb at least until the completion of the first envelope sheet.

Resting usually occurred after intranidal activities such as envelope and cell construction or grooming, and it was sometimes accompanied with turning around the pedicel. Some cases in which these behavioural elements were successively involved are as follows:

May 30, 1976 (5:38′00″–6:09′20″): R→W→R→W→R→Tp→R→Ln; June 4, 1976 (5:30′00″–6:09′07″): R→W→R→W→R→W→Ci→G→R→W→Ln; Same day (7:15′45″–33′52″): Rn→Cp→Ec→W→G→Ci→R→W→Ln; Same day (9:42′10″–10:03′21″): Rn→Cp→Lr→Ec→G→Ci→R→W→G→R→W→G→Ci→Ln. (Ci, cell inspection; Cp, chewing pulp; Ec, envelope construction; G, grooming; Ln, leaving nest; Lr, hind-leg rubbing; R, resting; Rn, returning to nest; Tp, turning around the pedicel; W, walking about on the comb)

3.3.4. Other intranidal activities. Oviposition was observed only once, on May 30 in Nest A7612. The foundress came back to the nest with pulp (16:07′37″), started envelope construction (07′49″), walked about on the comb and inspected three cells consecutively (09′35″), and rested in the posture mentioned above (10′00″). Then she suddenly appeared on the comb and walked about (16′00″), then laid an egg into a newly built cell (17′00″–21′00″). Then she left the nest to

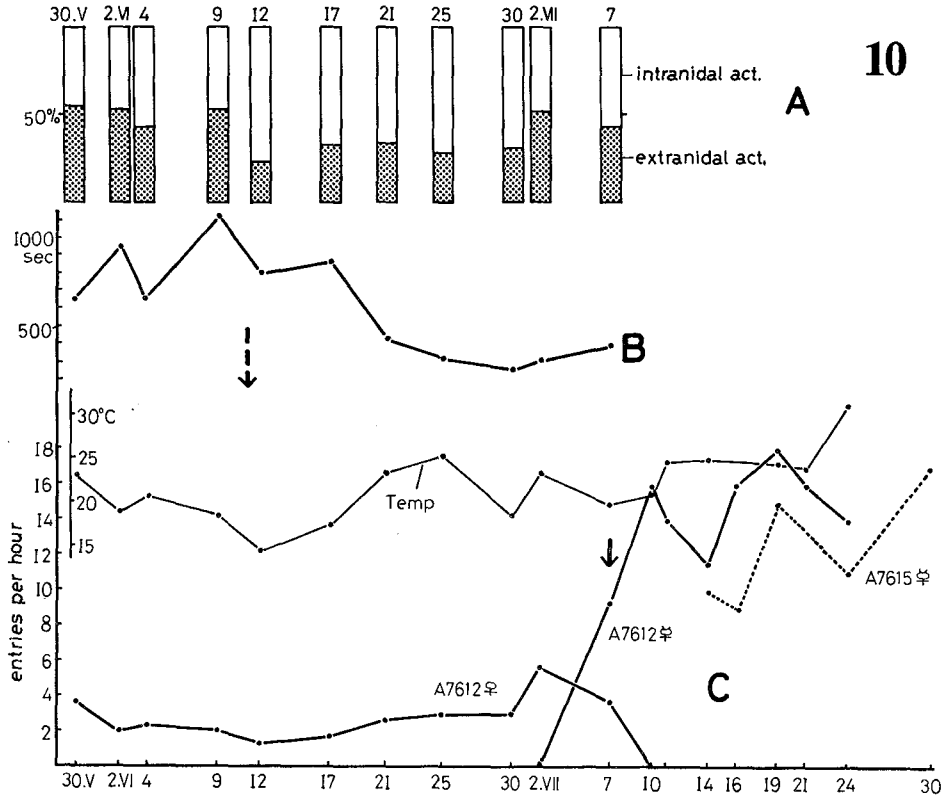


Fig. 10. Extranidal activities of *V. analis insularis* foundress during first 40 days from nest initiation (A7612). Observations were largely made within the period from 10:00 to 14:00. A. Change of intra- and extranidal activities in percentage of time spent in each; B. Change in mean duration of foraging trips; C. Changes in the number of entries into the nest by foundress (A7612♀) and by workers (A7612♀ and A7615♀). (→ denotes the co-operation of the foundress and workers in foraging, and - - → completion of the first envelope sheet.)

forage at 22'20".

Cell inspection was frequently observed after cell or envelope construction, or between restings. But its meaning is not known to us.

Grooming was classified into two distinct categories. One was hind-leg rubbing which was observed when the foundress returned to the nest with pulp and chewed it; the other was the rubbing of antennae, head and the dorsal part of thorax with fore and mid legs.

Brood nursing could not be observed because the comb was obscured by the envelope during nursing period.

3.3.5. Daily activity. In Nest A7612 daily activity of the foundress was observed on May 30 and June 4, 1976 (Fig. 9). On May 30 extranidal activities had already begun when we started observation (6:00) and lasted till sunset. During the first two hours (6:00–8:00) only one trip was made by the foundress in each hour, with low percentages of time spent in extranidal activities. But the

number of trips increased (2–5 per hour) from 8:00 on, always with higher ratios of time spent in extranidal activities (52.5–87.4%). Extranidal activities amounted to 60.68% of the total observation time. On the other hand, on June 4 extranidal activities were very low (1–3 trips, 28.4–60.5% in each hour from 8:30) in comparison with those on May 30, possibly owing to the low temperature of that day. Intranidal activities conversely amounted to 62.62%. Cell and envelope costruction were observed throughout the active period.

3.3.6. Extranidal activities during first 40 days. The mean number of trips made by the foundress per hour was 1.3 to 3.7 during the first month, but on July 2 it increased to a maximum of 5.2 and then decreased, and trips ceased on July 10. On July 7 when trips by workers were first observed, the foundress also made trips as usual (Fig. 10C). This suggests the co-operative stage in this species, though it seems to be short in comparison with that observed by Matsuura (1974) for *V. crabro flavofasciata*, or by Verlaine (1932) for *Vespula*. The time spent in extranidal activities by the foundress was under 60% throughout, and especially in remarkably low ratios during about a month after the completion of the first envelope sheet (Fig. 10A). The mean duration of each trip was generally long and variable until June 17 (656.4–1123.2 sec.), but from June 21 on decreased significantly and was stabilized at about 300 to 400 seconds. Figure 11 shows the number of trips plotted against the duration of each trip on May 30 (A) and from June 21 to July 2 combined (B). From this figure it is clear that on May 30 the trips considerably varied in duration, though a peak was reached at the class between 300 and 500 seconds. On the other hand, from June 21 to July 2 trips were confined to within 700 seconds with one exception (1335 sec.). This may have contributed to the drop and stabilization of the mean time for a single trip during 20 days from June 17. It seems that trips taking much time during late May and early June were for sucking tree sap.[1] On these trips, however, the foundress might have often gathered wood pulp on her way home. It must be noted that the trips other than those for gathering wood pulp or protein food, while rarely observed during late May and early June, were fre-

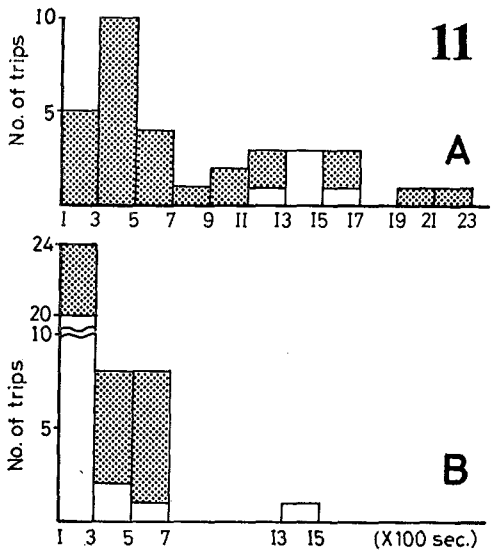


Fig. 11. Number of trips by *V. analis insularis* foundress against time spent in a single trip (A7612). A: May 30, 1976; B. June 21 to July 2 combined. Dotted: returned with pulp; Blank: with honey or none.

1) According to Matsuura (1969) fertilized *Vespa* females are observed to take tree sap from oaks only for a short period after hibernation and they disappear therefrom in parallel with the commencement of nest foundation. But later, he wrote that the foundress depends almost entirely on tree sap for her food until the eggs hatch.

quently made during late June and early July (Fig. 11: blank). The reason for this is not known to us.

3.4. Mature nest and productivity

3.4.1. Nest contents

1) *V. analis insularis.* Six mature or dissolved nests collected from late August to early October in Sapporo were examined (Tables 1, 3). Out of them four mature nests collected in early to mid-September had lost the foundress. The number of workers ranged from seven to 35. Males had emerged in all the nests (6–56), while new queens were seen in Nest A7511 (Sep. 4) alone. Males were mainly reared in the first and second combs — counted from the top (i.e. from the uppermost comb) — and new queens in the second and third. Eggs, larvae and cocoons were abundant during August but decreased in September. The cell map of a typical mature nest is given in Fig. 12. The larva: worker ratio varies from nest to nest (2.80–6.04). Nests collected in October contained neither adults nor immatures. In Nest A7409 (Sep. 7) and A7410 (Sep. 17) no queen adults nor pupae were found, while Nest A7618 and A7619 (Aug. 21) had 15 and 20 queen pupae, respectively. It seems that no new queens have been produced in the former two nests. On the other hand, many queen adults and pupae were found in Nest A7511 (Sep. 4). All the fifth instar larvae of this nest were also regarded as new queens on the basis of body size. Thus, this nest brought up only new queens, except for some males already produced.

The nest with envelope reached a maximum of 15.0×18.5 cm in diameter (Table 1). The number of cells composing the first comb was 80 to 110, being less than that in the second comb (70–155) with the exception of Nest A7410 (80:70), a dwarf nest probably due to the loss of the foundress in an earlier nesting stage. The third comb usually remained half-built and comprised 14 to 165 cells. Only one nest (A7511) had a fourth comb comprising 20 cells. The total number of cells ranged from 150 to 441, but it was usually confined to 230 to 310 (Tables 3, 4).

2) *V. mandarinia latilineata.* The nests (Mn7301 and Mn7602) were collected in late August and mid-September (Tables 1, 3). The number of workers was 110 and 184, respectively, and in Nest Mn7602 a few males and new queens had emerged. The foundress was active and many eggs and larvae were found over all the combs in either nest. Workers were reared in the first and second combs alone, and males and new queens in the first to fifth combs. Matsuura and Sakagami (1973) also reported a similar condition in Wakayama. Rearing new queens in the first comb usually does not occur in other Japanese vespine species.

3.4.2. Productivity

1) *V. analis insularis.* The total production of adults was estimated based upon the mature and dissolved nests. Estimates based upon mature nests may at times be somewhat inaccurate, but the data from some such nests gave us useful information to estimate the production of workers, males and new queens separately. The estimated number of adults which had emerged when the nest was taken is given in Table 3, and the estimated total number of adults produced is given in Table 4.

The total number of adults produced ranged from 141 to 352 with the exception of Nest A7410 (86), which was a dwarf nest due to the loss of the foundress. The number of workers produced was estimated for Nest A7409, A7410,

Table 3. Composition of brood populations and adult productivity of nests of of each brood stage present at

Comb no. from top	Cocoons					Larvae				
	♀	♂	♀♂	?	Total	5	4	3	2	1
A7409										
1					0	9				
2				8	8	12	5	3	2	2
3					0				2	1
Total				8	8	25	5	3	4	3
A7410										
1			4		4	22	2	1	2	1
2			5		5	18	9	9	8	8
Total			9		9	50	11	10	10	9
A7511										
1					0	6				
2	53				53	35		1	1	2
3	67				67	62	12	4	12	4
4					0				2	4
Total	120				120	103	12	5	15	10
A7618										
1		7	16		23	26	2	1	4	3
2	15		24		39	35	13	8	7	6
3									4	6
Total	15	7	40		62	61	15	9	15	15
A7619										
1			34		34	27	3	4	2	1
2	20		7		27	27	13	4	6	11
3					0					0
Total	20		41		61	54	16	8	8	12
A7621										
1					0					
2					0	1				
3				6	6	7				
Total				6	6	40				
Mn7301										
1		48	1	9	58	35	11	10	6	8
2		68	11	15	94	21	2	4	4	13
3	10		20	31	61	44	13	6	6	3
4					0	8	14	16	16	20
5					0					
Total	10	116	32	55	213	108	40	36	32	44
Mn7602										
1	3	58	23		84	11	3		1	
2	98		78		176	32	7	8	10	12
3	108		23		131	41	28	10	11	8
4				12	12	69	28	24	24	21
5					0		3	10	11	7
Total	209	58	124	12	403	153	69	52	57	48

1) Cells with supernumerary immatures (cf. Sk. Yamane, 1974). 2) E, E, (1); for 1st to 4th larval instars. Figures in parentheses show the number of cells.

V. analis insularis and *V. mandarinia latilineata* from Sapporo. (Data are numbers time of collection of the nest.)

Total	Eggs	Empty cells	s[1)]	?	Total no. of cells	Estimated no. of adults produced
9	0	86	0		95	83
24	0	90	0		122	29
3	0	11	0		14	0
40		183			231	112
28	0	48	0		80	37
52	5	8	0		70	0
90	5	51	0		150	37
6	0	95	0		101	81
39	0	63	0		155	55
94	0	4	0		165	0
6	9	5	0		20	0
145	9	167	0		441	136
36	15	16	1		91	56
69	1	4	0		113	0
10	20	0	0		30	0
115	36	20	1		234	56
37	20	19			110	62
61	22	0			110	0
0	14	0	0		14	0
98	56	19	0		234	62
0	0	97	0		97	
1	0	125	0		126	
7	0	67	0		80	
40	0	257	0		303	
70	22	33	1[2)]		184	148
44	23	6	4[3)]	3	174	57
72	14	3	1[4)]		151	2
74	44	3		8	129	0
0	35	2			37	0
260	138	47	6	11	675	207
15	0	175	0		274	286
69	23	71	0		339	106
98	5	?	0		234	0
166	44	13	1[5)]		236	0
31	25	1	1[6)]		58	0
379	97	260	2		1141	392

3) E, E (3), 1, 1, 4 (1); 4) E, 1 (1); 5) 2,3 (1); 6) 1,1 (1). E stands for egg, and 1–4

Table 4. Estimated productivity in nests of *V. analis insularis* and *V.* of cells differ slightly from the corresponding

Comb no. from top	Diameter of comb (mm)		No. of
	long	short	No. of times of production
			0	1
A7203[1)]				
1	92.5	86.0	12(12.8%)	67(71.3)
2	108.0	107.0	42(34.1)	81(65.9)
3	90.0	89.5	60(65.9)	31(34.1)
Total			114(37.0)	179(58.1)
A7409				
1	90.0	84.5	23(24.2)	52(54.7)
2	94.0	93.5	73(59.8)	49(40.2)
3	32.0	30.0	14(100.0)	0(0)
Total			110(47.6)	101(43.7)
A7410[2)]				
1	75.0	70.0	29(36.2)	39(48.8)
2	70.0	65.0	47(67.1)	23(32.9)
Total			76(50.7)	62(41.3)
A7511				
1	90.0	85.0	29(28.7)	66(65.3)
2	130.0	120.0	12(7.7)	142(91.6)
3	110.0	110.0	36(21.7)	130(78.3)
4	40.0	35.0	20(100.0)	0(0)
Total			97(21.9)	338(76.5)
A7618				
1	84.0	79.0	12(13.0)	56(60.9)
2	87.5	87.0	38(33.6)	75(66.7)
3	41.5	39.0	30(100.0)	0(0)
Total			80(34.0)	131(55.7)
A7619				
1	89.5	88.5	1(0.9)	94(82.7)
2	88.0	84.5	56(50.9)	54(49.1)
3	26.5	26.5	14(100.0)	0(0)
Total			71(30.3)	145(62.0)
A7621				
1	70.0	69.5	20(20.6)	59(60.8)
2	100.5	98.0	43(34.1)	83(65.9)
3	78.0	75.5	73(91.3)	7(8.7)
Total			136(44.9)	149(49.2)
A7622[1)]				
1	88.5	85.0	8(8.5)	77(81.9)
2	82.0	74.0	28(29.2)	68(70.8)
3[4)]	36.5	35.0	15(57.7)	11(42.3)
Total			51(23.6)	156(72.2)
A7623[1)]				
1	90.0	77.5	21(23.6)	58(65.2)
2	99.5	95.0	42(36.5)	73(63.5)
3	73.5	72.5	62(76.5)	19(23.5)
Total			125(43.9)	150(52.6)

mandarinia latilineata from Sapporo. (Some values in the total number ones in Table 3, possibly owing to miscounting.)

cells of adults in each cell: 2	3	Total no. of cells [A]	Total no. of adults produced [B]	No. of adults produced per cell [B/A]
14(14.9)	1(1.0)	94	98	1.04
0(0)	0(0)	123	81	0.66
0(0)	0(0)	91	31	0.34
14(4.5)	1(0.4)	308	210	0.68
20(21.1)	0(0)	95	92	0.97
0(0)	0(0)	122	49	0.40
0(0)	0(0)	14	0	0.00
20(8.7)	0(0)	231	141	0.61
12(15.0)	0(0)	80	63	0.79
0(0)	0(0)	70	23	0.33
12(8.0)	0(0)	150	86	0.57
6(6.0)	0(0)	101	78	0.77
1(0.7)	0(0)	155	144	0.93
0(0)	0(0)	166	130	0.78
0(0)	0(0)	20	0	0.00
7(1.6)	0(0)	442	352	0.80
24(26.1)	0(0)	92	104	1.13
0(0)	0(0)	113	75	0.66
0(0)	0(0)	30	0	0.00
24(10.3)	0(0)	235	179	0.76
18(16.4)	0(0)	110	127	1.15
0(0)	0(0)	110	54	0.49
0(0)	0(0)	14	0	0.00
18(7.7)	0(0)	234	181	0.77
18(18.6)	0(0)	97	95	0.98
0(0)	0(0)	126	83	0.66
0(0)	0(0)	80	7	0.09
18(5.9)	0(0)	303	185	0.61
6(6.6)	0(0)	94[3)]	89	0.94
0(0)	0(0)	96	68	0.71
0(0)	0(0)	26	11	0.42
6(2.8)	0(0)	216	168	0.78
10(11.2)	0(0)	89	78	0.88
0(0)	0(0)	115	73	0.63
0(0)	0(0)	81	19	0.23
10(3.5)	0(0)	285	170	0.60

Table 4.

Comb no. from top	Diameter of comb (mm)		No. of	
	long	short	No. of times of production	
			0	1
Mn7301				
1	174.5	125.0	6(3.2)	117(63.2)
2	179.0	136.0	4(2.3)	173(97.7)
3	183.5	138.5	43(28.7)	107(71.3)
4	159.0	144.0	125(94.7)	7(5.3)
5	77.5	71.0	37(100.0)	0(0)
Total			215(31.6)	404(59.3)
Mn7602				
1	230.0	190.0	5(1.8)	172(62.1)
2	270.0		45(13.1)	278(81.0)
3[4)]	250.0	240.0	62(26.5)	172(73.5)
4	240.0	210.0	157(66.2)	80(33.8)
5	105.0		58(100.0)	0(0)
Total			327(28.5)	702(61.1)

1) Nests taken after dissolution.
2) Dwarf nest probably due to the loss of foundress in an earlier nesting stage.

A7511, A7618 and A7619 (79, 28, 66, 63 and 62, respectively)[1)]. Males and new queens were also estimated as follows: —64♂ : 0♀ (A7410), 22:251 (A7511), 60:57 (A7618) and 54:47 (A7619). The number of cells used in different generations is given in Table 4.[2)] Over all the nests examined only one cell produced three generations and no cells produced four generations. Cells which produced the second generation were largely found within the first comb, ranging from 6.6 to 26.1% of the total cells of the first comb. The third comb usually had immatures, but sometimes produced no adults. The mean number of generations produced per cell[3)] sometimes exceeded 1.00 in the first comb, but always lay between 0.60 and 0.80 in all the combs combined. Cells which produced two generations occupied only 1.6 to 10.3% of the total cells.

2) *V. mandarinia latilineata.* The total number of adults produced was estimated at 530 for Mn7301 and at 944 for Mn7602 (Table 4). The number of workers, males and new queens produced was estimated at 423, 175 and 312, respectively, for Nest Mn7602.

1) These estimates are calculated as follows: Number of adults emerged − number of male and new queen adults present + number of worker pupae and final instar larvae present. In this case it is assumed that neither males nor queens had departed from nest and at least pupae and mature larvae of the worker could have grown into adults. The numbers of males and new queens are estimated in a similar way.
2) The term "generation" is used in the same sense as in Spradbery (1973, p. 180).
3) Here the number ($\bar{G}$) is calculated from the following formula:

$$\bar{G} = \frac{\text{estimated total number of adults produced}}{\text{total number of cells}}$$

It naturally differs from Spradbery's "percentage cell productivity", which is expressed by

$$\frac{(\text{number of brood present} + \text{total adults produced})}{\text{number of cells} \times 3} \times 100$$

Continued.

cells of adults in each cell: 2	3	Total no. of cells [A]	Total no. of adults produced [B]	No. of adults produced per cell [B/A]
60(32.5)	2(1.1)	185	243	1.31
0(0)	0(0)	177	173	0.98
0(0)	0(0)	150	107	0.71
0(0)	0(0)	132	7	0.05
0(0)	0(0)	37	0	0.00
60(8.8)	2(0.3)	681	530	0.78
98(35.4)	2(0.7)	277	374	1.35
20(5.9)	0(0)	343	318	0.93
0(0)	0(0)	234	172	0.74
0(0)	0(0)	237	80	0.34
0(0)	0(0)	58	0	0.00
118(10.3)	2(0.2)	1149	944	0.82

3) Some cells are not known for the number of generations produced.
4) Half-decayed comb, presenting incomplete data.

The maximum number of generations produced by a cell was three. Such cells were found only in the first comb (0.3 and 0.2%, in the two nests). Cells which produced twice were seen in the first and second combs, and attained 8.8 and 10.3% of the total cells in the two nests, respectively. The fifth combs of both the nests had immatures, which probably would not have been able to grow into adults.

3) *Discussion.* It has been known that *V. analis insularis* belongs to the "small population type" among the Japanese species of *Vespa* (Matsuura, 1973). In Wakayama Pref. it constructs one to four combs and 300 to 800 cells, and its colony produces 50 to 150 workers, 100 to 160 males and 100 to 150 new queens (Matsuura, 1976).

Although the number of combs built are practically identical in both the regions, our data indicate that the colony of this species in Hokkaidô tends to be smaller than that in Wakayama.

In Wakayama *Vespa mandarinia latilineata* builds nests much larger than those of *V. analis insularis* (Matsuura, 1973; Matsuura and Sakagami, 1973). We confirmed a similar tendency in Hokkaidô. Matsuura (1976) mentioned that in Wakayama the colony of this species usually comprises four to ten combs and 300 to 5000 cells, and that 514 workers, 617 males and 333 new queens emerged from the largest colony. Suzuki et al. (1961) report on three nests of this species from Kantô District, which possessed from six to eight combs.

4. Mature nest structure

4.1. Description of nest

4.1.1. V. analis insularis. The typical structure of the nest is shown in Fig. 14. Its envelope is nearly spherical, with the height: width ratio 1.1:1–1.3:1. Combs are completely enclosed by the envelope except for a small hole of the

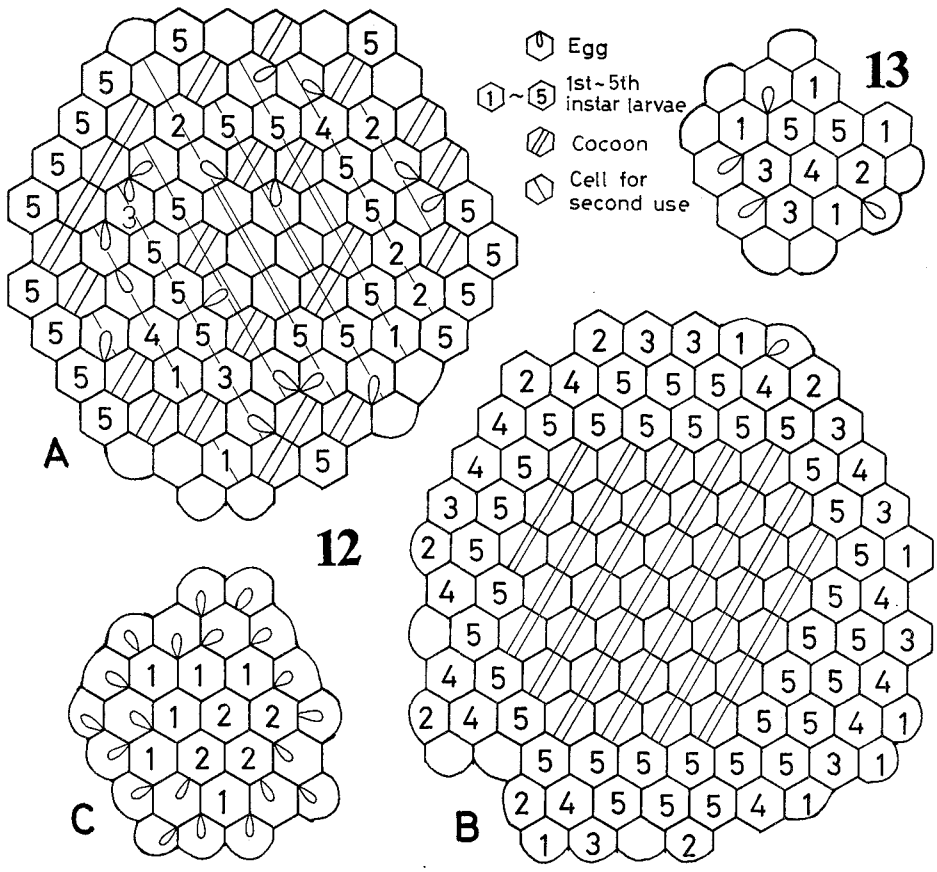


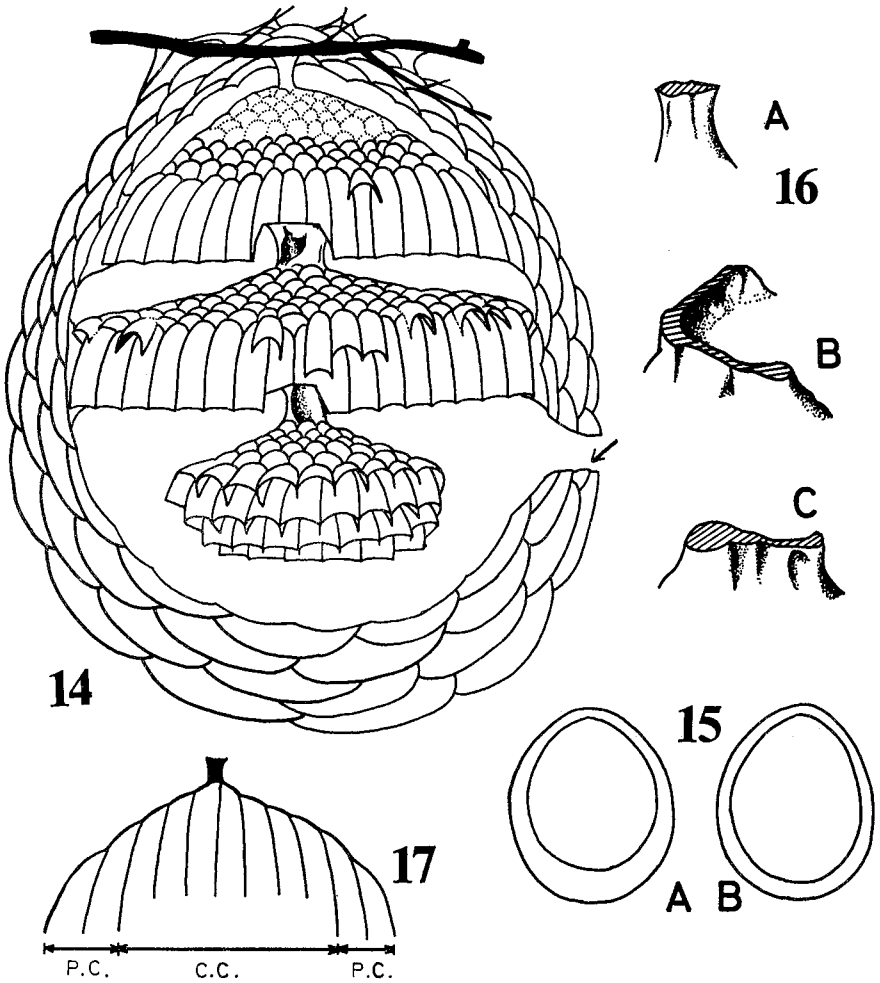
Fig. 12. Cell map of a typical mature nest of *V. analis insularis*. A–C. 1st to 3rd combs (counted from the top).

Fig. 13. Cell map of a young nest of *V. analis insularis* (A7408; Jul. 12, 1974, H. Katakura leg.).

entrance (15–20 mm in diameter), which opens in the middle or lower part of the nest. Air-filled chambers facing the entrance were closed with pulp in Nest A7409 and A7621 (Fig. 14, arrow). (This could not be confirmed in other nests on account of the damage done to the entrance when anesthetizing wasps.)

The envelope shows a well-known multilayered shell-like structure, involving many air-filled chambers among the layers. In the lower part of nest the envelope has more layers (5–6 sheets) and larger chambers than in the upper part (3–4 sheets). Envelope is 10–20 mm in thickness at the top (i.e. roof), 15–20 mm in the middle, and 20–30 mm at the bottom, with a slight variation among nests. Nest A7619 was exceptional with the envelope nearly identical in thickness throughout (Fig. 15, A *vs.* B).

Of nine mature or dissolved nests examined seven had three combs, one had four, and one had only two. Each comb is a more or less circular disk (diameter is given in Table 4). In profile first comb is inverted bowl-shaped; the second and third ones have a low conical roof, highest centrally where the mainstay is attached



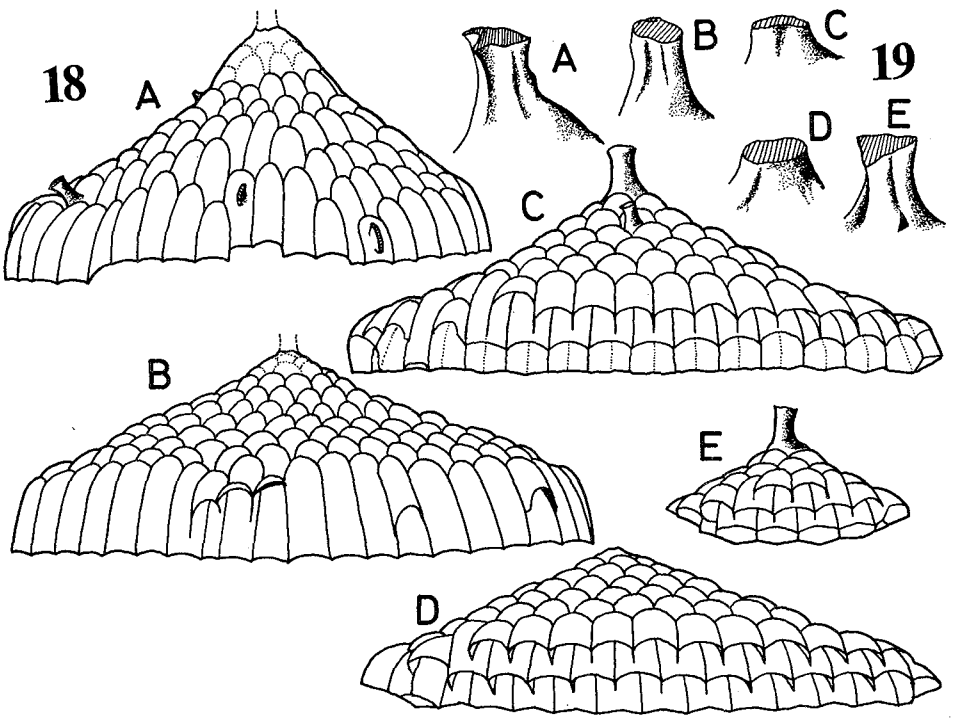
Figs. 14–17. Mature nest of *V. analis insularis*. 14. Typical mature nest, frontal half of envelope cut away, and the first and second combs partially cut away to show pillars; 15. Variation in the thickness of envelope. A: Normal envelope; B: Envelope nearly identical in thickness throughout; 16. Comb pillars (A. Mainstay; B,C. Mainstay with a ribbon-like structure); 17. Division of cells of the first comb into central (C.C.) and peripheral (P.C.) cells (cf. Fig. 20).

(Fig. 14). Cell bottoms are swollen out on the dorsal surface of the comb, giving the latter a rugged appearance. The margin of the first comb and/or second one is often partially or wholly connected with envelope, and some of marginal cells are sometimes sealed with carton.

Combs are connected with each other and the first comb with the roof of the nest by only one pillar, except for Nest A7619 wherein the first comb was connected with the roof by two pillars different in size. The pillars are divided into two types in shape. Type I: flattened columnar, 3–8 mm thick, represented by the pillar which connects the first comb with the roof and directly attaches to the

substratum (Fig. 16A). Type II: consisting of the mainstay and a ribbon-like structure 1–2 mm thick and extending from the mainstay (Figs. 16B, C).

4.1.2. V. mandarinia latilineata. The envelope is much reduced and incompletely covers the combs. (Matsuura and Sakagami (1973) state that the lowest comb is always exposed within the nest cavity.) Both the nests examined had five combs which are considerably larger than those of *V. analis insularis*. Combs are disk-like; first to third combs are elliptical and the fourth and fifth nearly circular in Nest Mn7301, their roofs presenting a rugged appearance as in *V. analis insularis*. In profile first comb is conical rather than inverted bowl-shaped (Fig. 18A); the lower combs are also conical but more shallow (Figs. 18B–E). Combs are connected to each other and the first comb to the roof of the nest by the mainstay as seen in *V. analis insularis* and often also by auxiliary pillars. The mainstay (Figs. 19A, B) is thicker (6–8 mm in thickness) than auxiliary pillars (1–4 mm; Figs. 19C–E); the latter is sometimes leaf-shaped. In Nest Mn7301 the numbers of auxiliary pillars were 9, 2, 1, 0 and 1 (counted from the top comb). Cell walls are clearly thicker than in *V. analis insularis*. The colour of carton is darkish brown in contrast with light brown in *V. analis insularis*.



Figs. 18, 19. Mature nest of *V. mandarinia latilineata*. 18. A–E. 1st to 5th combs (counted from the top); 19. Pillars, not to the same scale (A, B. Mainstay; C–E. Auxiliary pillars).

4.2. *Cell size*

It is apparent at a glance that cells constructed later are larger in diameter than those constructed earlier in both *V. analis insularis* and *V. mandarinia latilineata*. To examine this in detail, the diameters of ten cells selected at random from each comb were measured for the following nests: A7618, A7621, A7622 and A7623 (*V. analis*), and Mn7301 (*V. mandarinia*). In the first comb the central and peripheral zones were distinguished (Fig. 17), because the central zone is known to be built by the foundress and the peripheral by workers. Each cell was measured for diameter at the widest part and in such a manner as to exclude from measurement the influence of cocoon lining (Fig. 20).

There were significant differences in cell size among combs and between the central and peripheral zones of the first comb in both the species (tested by F-test; $p<0.01$) (Fig. 20). In *V. analis insularis* the first comb is mainly used to rear workers and the second and third sexuals (males and new queens). The difference between the central and peripheral cells well corresponds to the seasonal change in adult worker size. This is also true of *V. mandarinia latilineata* in which workers are produced from the first and second combs as stated above.

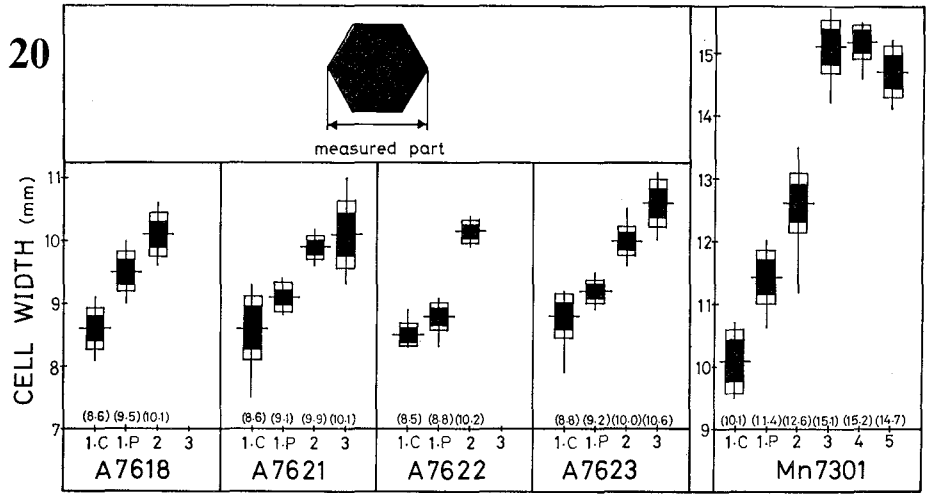


Fig. 20. Cell width in some nests of *V. analis insularis* (A7618, A7621—A7623) and *V. mandarinia latilineata* (Mn7301). Figures in parentheses show the mean value. 1–5. 1st to 5th combs; 1.C., 1.P. Central and peripheral cells of the first comb (cf. Fig. 17).

5. Notes on vespine embryo nests

The vespine embryo (queen) nests are basically uniform in structure, that is, with a pedicel, a comb and one or more envelope sheets, but somewhat variable in detailed structure, and shape and building manner of envelope. The embryo nests as well as mature nests also differ in the building material used. Some characters of the embryo nest are peculiar to this stage and sometimes differ among species, species groups or genera.

Duncan (1939) describes the embryo nests of some North American species and discusses specific and generic differences. He lays emphasis upon the manner of

attachment of the second and subsequent envelope sheets in comparing the embryo nests of *Vespula* with those of *Dolichovespula*. Matsuura (1971b) was the first to classify vespine embryo nests according to the external appearance (bowl-, ball-, and flask-shaped) and the number of sheets (single- and plural-sheeted), mainly based upon the Japanese *Vespa* species. He also referred to generic differences in the shape of the pedicel. Sk. Yamane (1976) used some of these characters in reconstructing vespine phylogeny.

In this section we will describe the embryo nests of some vespine species and try to interpret some important characters from taxonomic and biological viewpoints.

5.1. Description

5.1.1. Genus Vespa. Nest material is brittle, and brown or buff in colour. Pedicel is club-shaped, without a twist; hanging sheet for pedicel is not constructed. The envelope is single-sheeted (*V. analis*, *V. mandarinia*, *V. crabro*, *V. tropica* and *V. affinis*) or plural-sheeted (*V. xanthoptera* and *V. simillima*[1]); the first sheet is started from the substratum, and is never attached to the pedicel at some distance from the base; the second and later sheets, if constructed, are attached to the preceding ones (*V. xanthoptera*; Matsuura, 1971b) (Fig. 21), or the second sheet to the substratum and from the third on each to the preceding one (*V. simillima*) (Fig. 24); external appearance varies from bowl-shaped (*V. mandarinia* and *V. tropica*), through ball-shaped (*V. crabro*, *V. xanthoptera* and *V. simillima*) to flask-shaped (*V. analis* and *V. affinis*).

Some intraspecific variations are known in the embryo nests of *V. crabro* and *V. analis*. According to Duncan (1939, p. 133) *V. crabro* varies its nest-building behaviour according to the nature of the nest site. He says, "When nests are built in the open, or in cavities in soft earth, envelopes are built around the combs essentially as with nests of *Dolichovespula*. Nests built in hollow trees often are provided with no envelopes at all". However, in Japan the embryo nest of *V. crabro* always has a spherical envelope regardless of the nesting site (Matsuura, 1971b). As mentioned in *3.2.* the vestibule of *V. analis* embryo nests may vary in length in different localities.

5.1.2. Genus Vespula. The nest material is brittle and brown (*V. vulgaris* and *V. lewisi*), or pliable and grey (*V. rufa schrenckii*). The pedicel is club-shaped and elongate (*V. vulgaris*), or flattened, widest at the base so as to form a triangle (hanging sheet), with the lower portion twisted (*V. lewisi* and *V. rufa schrenckii*). The envelope is plural-sheeted; the first sheet is started in the middle of the pedicel, never from substratum; the second is attached nearly at the base of pedicel; the third to the pedicel slightly above the second or directly to the second sheet; the fourth and later each to the preceding sheet. The external appearance always ball-shaped.

5.1.3. Genus Dolichovespula. The nest material is pliable and grey. The pedicel is flattened, widest at the base so as to form a triangle; the lower portion is twisted. The envelope is plural-sheeted; the first sheet is started from the lower portion of the pedicel, the second attached somewhat above the first, the third and later sheets each to the preceding sheet (*D. sylvestris*), or each to the

1) Recently, *V. xanthoptera* and *V. simillima* have often been regarded as geographical races of the same species, for which Matsuura (1976) adopts the name *V. mongolica* André following van der Vecht (1959).

pedicel as is the second sheet (*D. saxonica* and *D. media*); external appearance is ball-shaped or flask-shaped (some cases in *D. media media* and *D. maculata*).

Though the number of sheets varies among individuals of the same species (e.g. *D. sylvestris*; Brian and Brian, 1948), generally five to six sheets are finally constructed. In the European *D. media media* and the Nearctic *D. maculata* the nest entrance is often developed downwards to form a long vestibule as seen in *Vespa analis* (Rau, 1929; Bohart and Bechtel, 1957; Kemper und Döhring, 1967), while *D. media media* in Hokkaidô does not construct a vestibule, though a slight projection is sometimes added to the entrance. *D. sylvestris* and *D. saxonica* also construct such a projection (Figs. 29, 32; see also Kemper und Döhring, 1967).

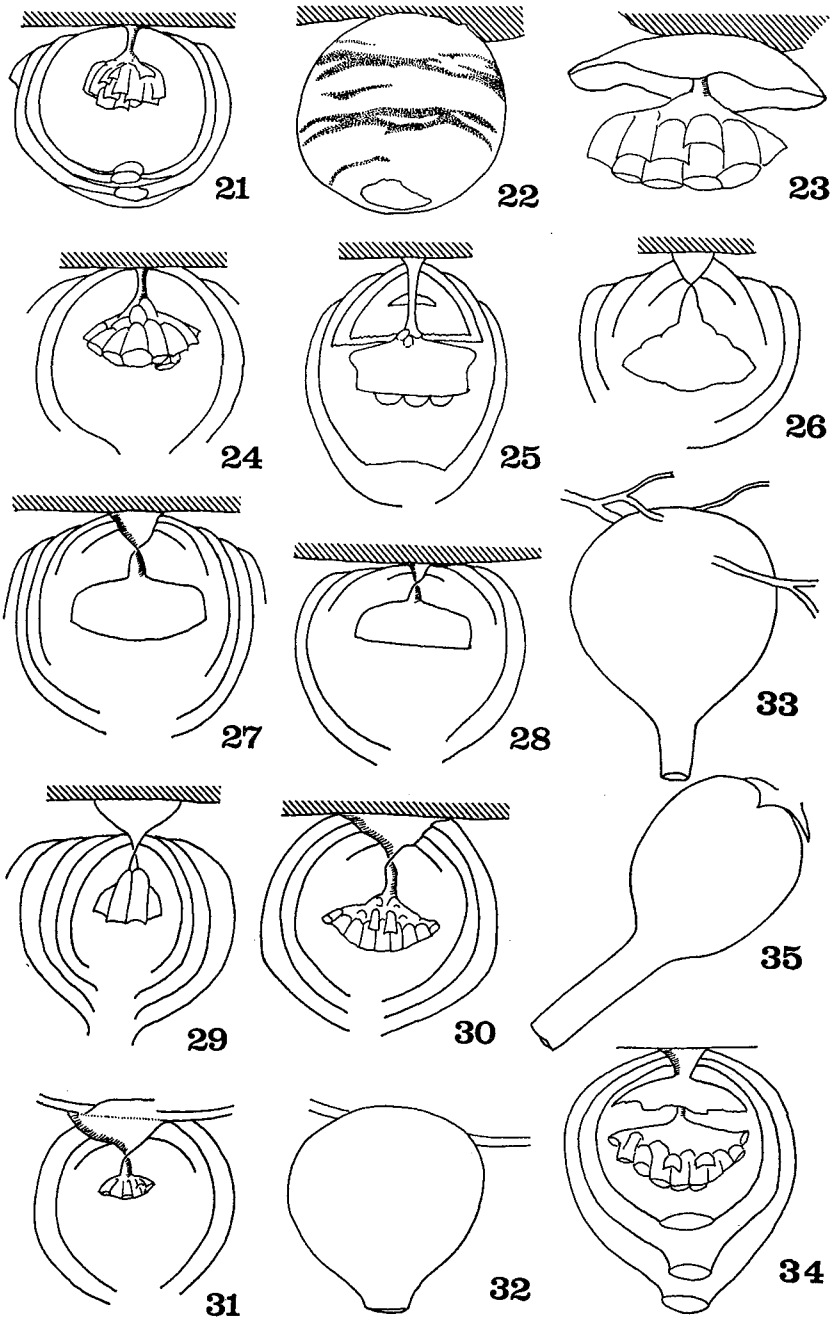
5.2. Roles of envelope

Vespa mandarinia and *V. tropica* construct embryo nests with an envelope sheet which never encloses the comb (Matsuura, 1971). They are subterranean in nesting and mainly distributed from the southern temperate zone to the tropics. The subterranean habit may reduce losses due to certain predators. Furthermore, the nests may secure sufficient warmth because of the subterranean habit and the warm climate even during early nesting period. Such conditions may allow these species to omit a complete envelope. On the other hand species such as *V. xanthoptera* and *V. simillima* which build nests in either open or enclosed sites in the temperate region build envelopes of many layers, probably for thermoregulation and as a defence against predators. As mentioned earlier, *V. crabro* with a similar nesting site preference often builds no envelope when nests are built in hollow trees or in very hard and stony ground (Duncan, 1939). The twig-nesting *V. analis* and *V. affinis*, mainly subtropical or tropical in distribution, have nests with a single sheet completely enclosing the comb.

The *Vespula* species, largely temperate in distribution and often subterranean in nesting habit, make a nest with many envelope sheets. Iwata (1971) considers that the main purpose of this kind of multilayered envelope is to avoid any direct contact between the comb and the [mud] roof at the top of the cavity. The thermoregulating effect is probably also important. Embryo nests of these species do not vary in structure according to the nesting site.

The multilayered envelope in twig-nesting species of *Dolichovespula* undoubtedly serves mainly as a protection from the wind and low temperature in heavy weather, with a minor role of protecting against predation. The difference in the manner of envelope multiplication between *Vespula* and *Dolichovespula* cannot be well explained, while the difference in material between them is easy to understand except in the case of *V. rufa* (Sk. Yamane, 1976). It can be said, however, that under weather-beaten condition it is more advantageous to start the second and later sheets separately from different points of the pedicel or directly from the substratum, as adopted by *Dolichovespula*. In this respect it must be noted that among *Vespa* species, some of which found nests in open places, the envelope is started directly from the substratum so as to increase its area of attachment.

The long vestibule built by *Vespa analis*, *V. affinis*, *Dolichovespula media* (in Europe) and *D. maculata* has several possible adaptive values, and the defence against the predator may be its primary role (Sk. Yamane, 1976). *V. analis* and *V. affinis* are essentially subtropical or tropical species and usually build nests on tree twigs relatively near the ground. Such a site may be frequently patrolled by ants,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which are serious predators of social wasps, and the long vestibule may well serve as a protection against them.[1] The diminution of the vestibule in *V. analis* in Hokkaidô, the northern limit of this species, can be explained as a response to reduced ant predation pressure. On the other hand, if the thermoregulation is concerned, the vestibule must be exaggerated in northern localities. *D. media* and *D. maculata* extend rather southwards or to plains in comparison with other congeneric species except for *D. sylvestris* (cf. Miller, 1961; Guiglia, 1972) and sometimes construct the vestibule. This supports our assumption. However, if the assumption is correct, nests with a long vestibule must be found, in these species, more frequently in the southern region. At present data on this point are not available. Nests of *D. maculata* with long vestibules were collected from New Hampshire (Jeanne, personal communication), Missouri (Rau, 1929), Ohio (Duncan, 1939) and California (Bohart and Bechtel, 1957). Furthermore, the lack of a distinct projection of the nest entrance in *D. sylvestris*, which sometimes extends more southwards than *D. media*, does not appear to support this assumption.

5.3. Some characters of taxonomic importance

In his discussion on the generic difference between *Vespula* and *Dolichovespula*, Duncan (1939) argues that in queen nests of the genus *Vespula* the second envelope sheet may be started before the first is completed, and similarly for later sheets. His assumption seems to have been based only on collected nests and indirect evidence. For instance, he says "The writer collected a small nest of *Vespula pensylvanica* .... which possessed two envelopes. The first extends downward but three-eights of an inch on one side and not over five-eights of an inch on the other. The second is much larger, being a full inch...." He cites three other nests with a similar condition. Although these conditions really exist, we do not consider them as supporting his argument. Envelope sheets constructed earlier are usually later broken down and used as material for other parts of the nest when later sheets are completed. Nests with such a condition are frequently found also in *Dolichovespula* (Figs. 30, 31, 34; see also Kemper und Döhring (1967), Abb. 29). Thus, Duncan's discrimination of *Vespula* from *Dolichovespula* based on the mode of envelope construction is inappropriate.

As mentioned above (*5.1.*), a true generic difference between *Vespula* and *Dolichovespula* lies in the manner of multiplication of the sheets, with the exception of *Dolichovespula sylvestris*, in which the envelope is built by the manner similar to that of *Vespula*. Though in this respect the embryo nests of *Vespa xanthoptera*

1) Recently this line of reasoning has been developed by Jeanne (1975) on the nest structure of social wasps.

Figs. 21–35. Vespine embryo nests (frontal half of envelope cut away except for Figs. 22, 23, 32, 33 and 35 showing external appearance), not to the same scale. 27, 28, 30–32 and 34. original; others redrawn from several authors. 21. *Vespa xanthoptera* (Matsuura, 1971b); 22. *V. crabro flavofasciata* (Matsuura, 1971b); 23. *V. tropica pulchra* (Matsuura, 1971b); 24. *V. simillima* (S7623, N. Azuma leg.); 25. *Vespula* (*Paravespula*) *vulgaris* (Janet, 1903); 26. *V.* (*P.*) *lewisi* (Shida, 1959); 27, 28. *Vespula* (*Allovespula*) *rufa schrenckii*; 29. *Dolichovespula* (*Metavespula*) *sylvestris* (Brian and Brian, 1948); 30–32. *Dolichovespula* (*Boreovespula*) *saxonica nipponica* (P7206, Np7414 and Np7416 (S. Aoki leg.)); 33. *Dolichovespula* (*Dolichovespula*) *media* (Kemper und Döhring, 1967); 34. *D.* (*D.*) *media media* (M7201, after worker emergence); 35. *D.* (*D.*) *maculata* (Bohart and Bechtel, 1957).

and *V. simillima* are similar to those of *Vespula*, the attachment point of the first sheet in the former is essentially different from the latter (Fig. 21 *vs.* 26).

The shape and mode of construction of the pedicel are also useful in the supraspecific classification. *Vespula* and *Dolichovespula* usually construct a hanging sheet before the pedicel (in a narrow sense) is constructed, whereas *Vespa* does not. The twisted pedicel[1] is seen in *Vespula* and *Dolichovespula*, but judging from Janet (1903) and Potter (1965), *Vespula vulgaris* constructs an elongate and club-shaped pedicel, without a distinct triangle base, very similar to that of *Vespa*. This character of the embryo nest has not been observed for its close relative, *Vespula germanica*.

5.4. Conclusion on embryo nest

Jeanne (1975) argues that a high level of ant predation, especially during the solitary stage of colony development, selects some manner for countering this force, and it is about at the tropics where most of the vespines drop out. The strictly haplometrotic nest foundation in the Vespinae, though advantageous for the individual queens if the colony is successfully established, is disadvantageous in the face of the more intense ant predation in the subtropics to tropics and even in the southern temperate zone. The underground nesting habit and the flask-shaped envelope seen in some *Vespa* species inhabiting these regions are probably adaptations to defence against ant predation. In southern Japan, *Vespa xanthoptera* often moves nests, after worker emergence, from the original closed place to an open place such as under eaves (Matsuura, 1976). This habit may reduce the danger from predation in the solitary nesting stage. The biological role of the envelope in *Vespula* and *Dolichovespula*, which inhabit the temperate region, may have largely been evolved in response to physical factors of the environment, with much reduced significance in defending nest contents from predators.

We must admit that the available information on the vespine embryo nests is still insufficient, especially for the members of *Provespa* and the subgenus *Allovespula* of the genus *Vespula*, and that we have not yet found biological significance for all important characters. Finally, we would like to emphasize that the study of social wasp nest structure should be carried out along the line shown by Jeanne (1975).

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1) Shida (1959) mentions that the triangular plate-like stalk which is screwed round by 90–180° skilfully absorbs the impact given to the nest when the comb is swung.

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(* Not directly accessible.)

PLATES

Plate I

Figs. 36, 37. Completed embryo nests of *Vespa analis insularis*.
36. A7616.
37. A7612.

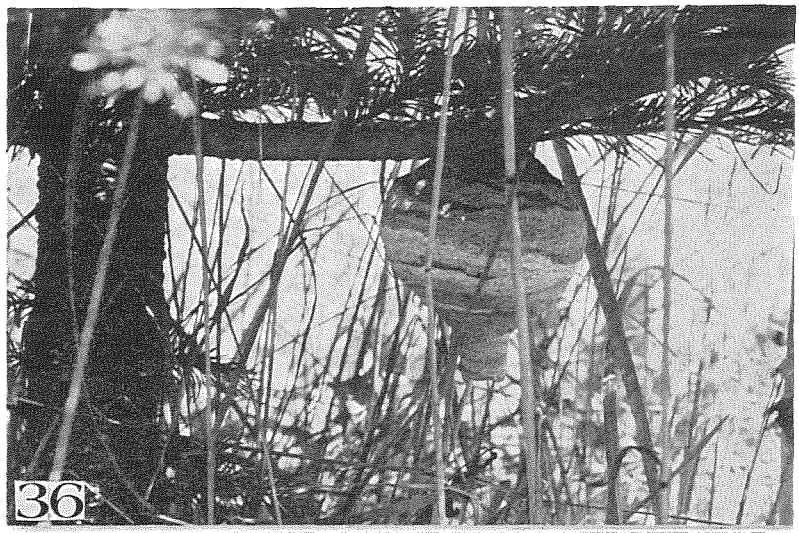
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Plate II

Figs. 38–43. Different stages of *V. analis insularis* nests, not to the same scale.

38. Initial nest with a foundress (A7612).
39. Completed embryo nest with a rather long vestibule (A7224).
40. Young nest (A7617).
41. Young nest (A7612).
42. Mature nest (A7621).
43. Mature nest (A7618), frontal half of envelope cut away.

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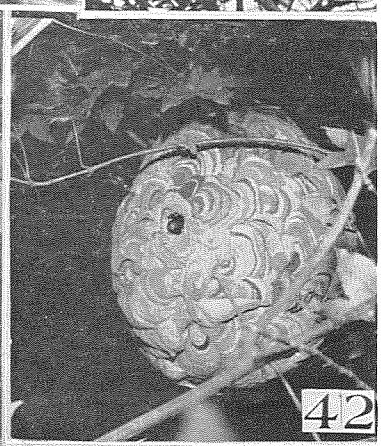
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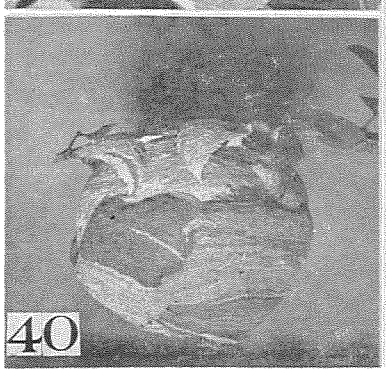
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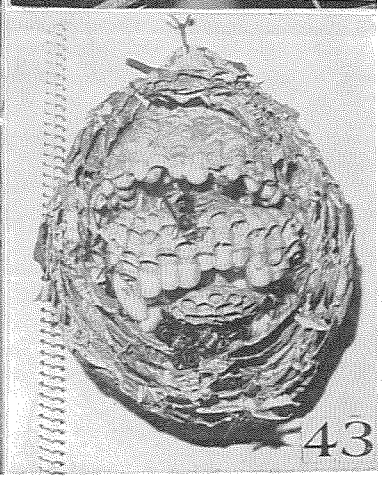
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