Ethological studies on the Japanese species of *Pemphredon* (Hymenoptera, Sphecidae), with notes on their parasites, *Ellampus* spp. (Hym., Chrysididae)[1]

By

Katsuji Tsuneki

(Zoological Institute, Faculty of Science, Hokkaido University)

(With 5 Text-figures)

As early as 1838, W. E. Shuckard recorded the habits of *Dineurus lethifer fabricii* Müller (=*Diphlebus unicolor* Fabr. et auct.). Since that time wasps of this group have been investigated relative to their bionomics by many entomologists as shown in the annexed list of literature. But the species dealt with by these observers is limited to only a few European representatives[2]. As for the indigenous species, *P.* (s. str.) *japonicus* and *Dineurus diervillae* were investigated by Iwata (1937) and recently Ohgushi published the observations on *D. lethifer fabricii*. With reference to the other 8 recorded species, however, nothing has been so far published. The present paper comprises the results of my study on all the known species of the genus occurring in Japan. Among them are included some species common to both Europe and East Asia. All the observations described here were conducted at Sapporo and Jôzankei, both in Hokkaido, with the exception of a a part relating to *D. diervillae*.

Before proceeding further I desire to express my indebtedness to Professor Tohru Uchida, for his kindness rendered during the course of the present study. My cordial thanks are also due to Assistant Professor Magoshiro Moritsu of Yamaguchi University, for the identification of the aphids captured by the wasps.

The hadits of members of this genus are comparatively monotonous. They are all hunters of aphids and their nests are made either in decayed wood or in ready-made tubes such as found in dried reeds, canes, grass halms and the like.

1) Contribution No. 284 from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan.

2) Five species out of eleven, viz. *lugubris* Latr., *lugens* Dahlb., *morio* V. d. Lind., *unicolor* Panz., and *lethifer* Shuck.

The structure of their nests belongs usually to the compound type, involving several brood-cells within, which are arranged, as a rule, in a branched form or a branched rosary form. But when made in tubes of reeds, canes etc., the cells are arranged inevitably in a lineal order. Partition walls between the cells are made of saw-dust particles scraped off from the inner wall of a gallery. In case an old nest is utilized, however, the material is sometimes mixed with dried aphids left in the cells wherein the egg did not hatch. As an interesting habit, the wasps usually make one or more spare tunnels in their burrow. These short blind tunnels are stuffed compactly with saw-dust until they are utilized as brood-chambers. When the wasps intend to close the tunnel leading to the cell which has been just completed, they are used to take necessary material out of such spare tunnels. As a rule, some of these tunnels are left unused after the completion of the nest. When finished, the brood-cell is packed compactly with aphids which are either deeply paralyzed or completely killed. The preys found in a single cell vary in number between some ten and about three scores. The number and kinds of victims tend to show a certain constancy with the species of wasps. Hunting is carried out on leaves or twigs of plants swarmed by a flock of aphids. The victim is either stung to paralysis or merely pressed to death between the mandibles. Transportation of the prey is always executed on the wing holding it with the jaws. Sometimes the wasps devour the preys for themselves, without carrying them to their burrows. During the course of provisionment the tunnel leading to the brood-chamber always remains open, without being temporarily closed as is usually done in other groups of hunting wasps. In one cell is deposited invariably a single egg which is glued to one of the preys. Oviposition is carried out after the provisionment of the cell is finished. The egg is, however, always found attached to the prey that is located either near the bottom or about the middle of the cell. On this account, it has hitherto been regarded by previous investigators that the egg is laid always in the course of provisionment of the cell. But such a concept seems to be incorrect, since in no case has the egg been found already deposited in the cells that have not been quite completed and provisioned. Probably the wasp, when the cell is fully stored with aphids, loosens the packed preys once more to force her way amongst them and lays her egg on the one that lies behind the middle of the cell; the manner is analogous to the case of the majority of Crabronids. The egg is attached to the body of the prey by its cephalic pole and is placed flat thereon along its bodily axis, the direction of its cephalic end being not always constant, although in most of the instances hitherto observed it has agreed with that of the pedestal insect. Sometimes the caudal end of the egg is protruded more or less beyond the body of the prey. The hatched larva begins at once to suck the juice from the pedestal-aphid. The next several victims are also sucked by the larva. But later, the larva devours the victims voraciously one after the other. Sometimes the larva looks very blackish.

Doubtless the colour is derived from the blaskish aphids injested. Very frequently the egg does not hatch, many cells being found stuffed with aphids which have already been dried up or covered with moulds, while the wasp is still engaging in the provisionment of the later cells of the same nest. It seems likely that in most of such nests the larva dies soon after hatching out, owing to the unfavourable status of the victims. But in some cases, late in the season, there is reason to presume that the wasps do not lay their eggs in some of the provisioned cells. Because it has been known in other groups of hunting wasps that the fruitless work for

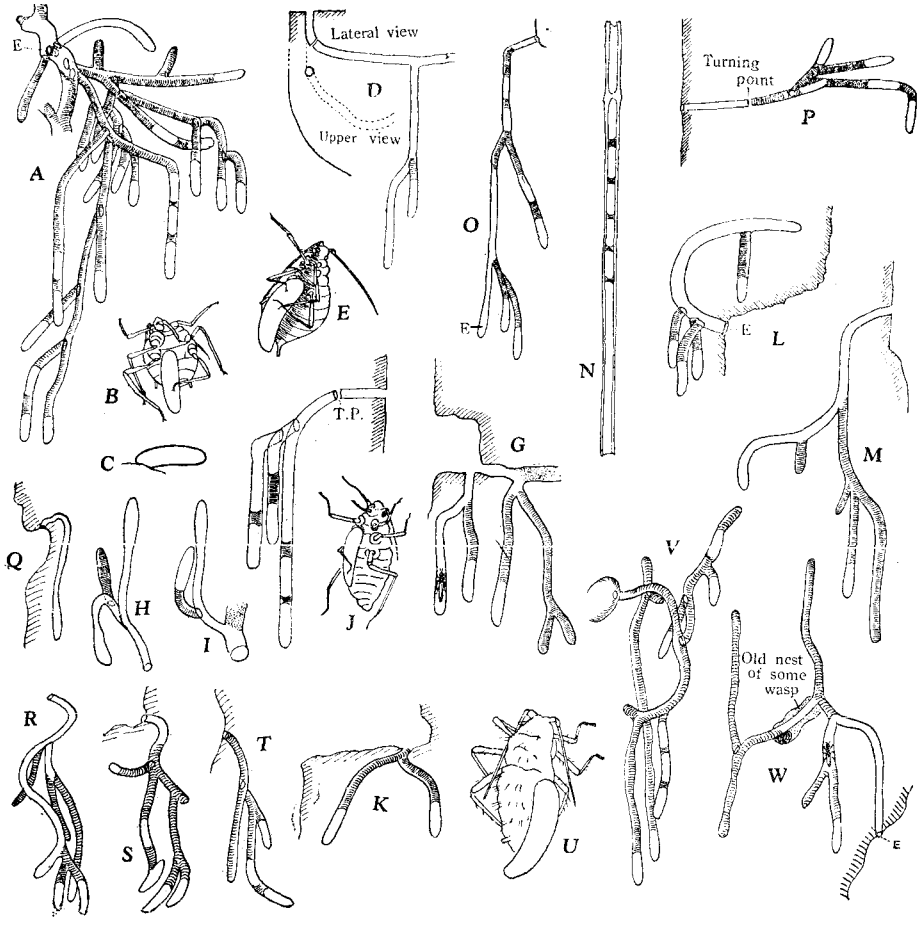

Fig. 1. Nests and some instances of manner of attachment of the egg in *Pemphredon* (detailed accounts are given in the text). E..Entrance, T. P..Turning point.

nesting is still continued automatically by the wasps even after the eggs to be laid are already exhausted in their ovaries.

The cocoon is usually very thin in structure and semitransparent. In form it is made generally in conformity with the space of the brood-cell, although in the case of large cells a considerable space is left empty at one end. Sometimes the cocoon consists of a layer of a dried substance of silken liquid smeared on the inner

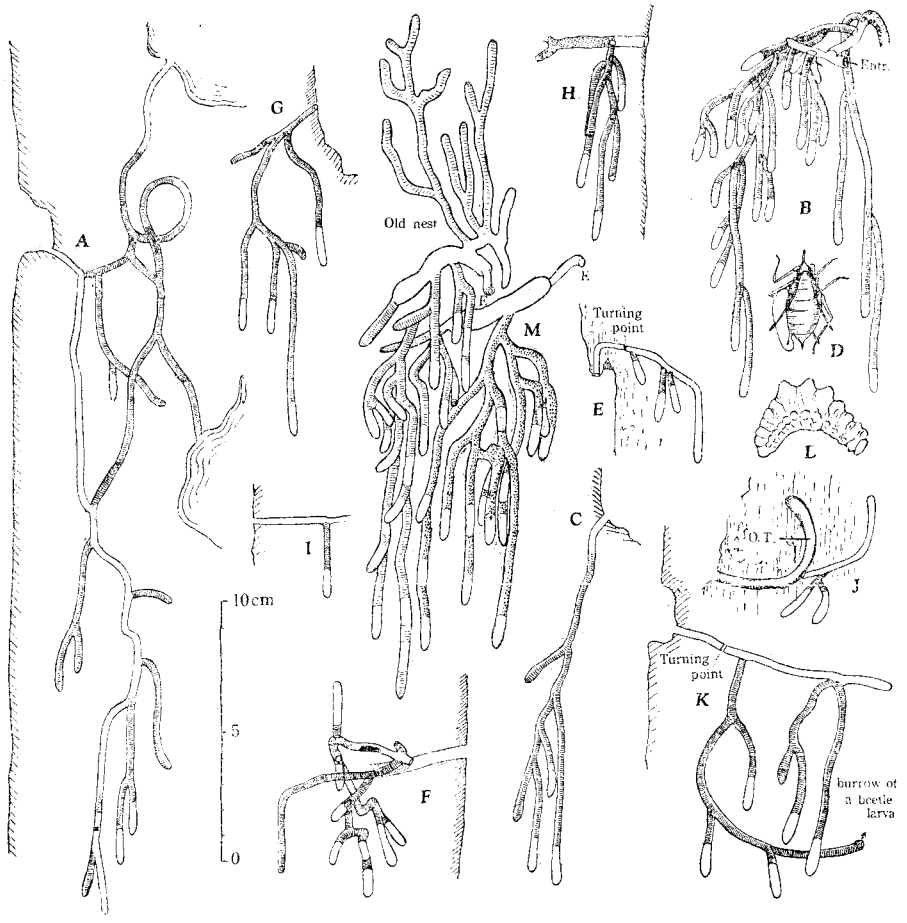

Fig. 2. Nests of *Pemphredon*. (detailed explanations are given in the text); D — an egg of *P. unicolor* attached to an aphid; L — a larva of *Ellampus auratus* L. O. T.. Old tunnel of some Crabronid.

wall of the cell. In such a case, it can hardly be torn off from the wall of the chamber. Mass-excretion of the larva is usually done prior to spinning of the cocoon. A comparatively hard cot is excreted in small lumps in succession, a phenomenon rather exceptional in the world of the hunting wasps. The larva in this developmental stage is capable of moving about with considerable activity by means of a peristaltic movement. At times when the partition tampon is loosely constructed and is less thick, it occurs that the larva bores through it and rests in the adjacent cell. After turning into the prepupal stage the body of the larva of some species becomes markedly orange or vermilion in colour, as pointed out by such early authors as Lichtenstein (1874) and Labourbéne (1875). In this stage also the larva is able to move its bodily parts, especially the caudal region, farily actively in response to the mechanical stimulus, excepting for the hibernating ones. After turning into the pupal stage the vermilion coloration in such forms as mentioned above is still retained for some time. However, gradually it fades away as development proceeds and is reduced to the original cream yellow coloration. Then the dusky colour of the imago begins to appear.

The wasps of this genus usually emerge twice a year, viz. early in summer and in autumn. But it seems likely that some of the small forms are able to repeat three generations a year. Other species (e.g. *flavistigma*) pass only one generation. The wasps that appear late in summer or in autumn continue to work as late as the end of October, when the air temperature lowers in the morning to 2°–5° C in Hokkaido, and no other wasps remain living. Hibernation is always carried out in the prepupal stage.

The sting of the adult wasps can not pierce the human skin even when captured between the fingers, although they would assume a posture of stinging. But they give off a sort of offensive odour much like that of ether, probably deriving from the aphids they have devoured. The wasps of this genus are most frequently found on leaves of *Sambucus* trees in the sunny hours of a day. There they lick the honey dews sprinkled by aphids or visit the honey glands of the young branches.

From the ethological point of view, no essential difference can be found between subgeneua *Pemphredon* and *Dineurus*. On the other hand, another subgenus *Ceratophorus*, at least in the species occurring in our region, is quite distinct in having parasitic habits. Between species there can be admitted more or less difference as to the structure of the nest, the number and species of the preys, modes of hunting etc.

1. **Pemphredon (Pemphredon) japonicus** Matsumura

As for the bionomics of this species detailed information was given by Iwata in 1937 and little remains to be added at present. So far as has been observed by me, the nests of this species are burrowed in decayed wood of standing tree or

of old telegraph poles as well as of piled-up logs. When the conditions are favourable a number of wasps gather within a limited nesting ground and form a crowded colony. To facilitate the digging work, the wasp tends to avoid the excavation of the hard tissue of the outer layer of the tree. For this reason, before beginning the nesting activities the wasp is used to search for ready-made holes such as the wood-pecker's excavation or the abandoned tunnels of other boring insects. In the case when the nest is made in the piled-up logs the wasp prefers to dig in from the cut end. Similar habits seem to be common among the members of the genus, resulting sometimes in the incidental utilization of an old nest. But even in the last-mentioned case, most of the wasps show a tendency to utilize only the entrance gallery, digging their own tunnels for themselves.

Three of their nests are illustrated in diagrams L and M of Figure 1 and diagram K of Figure 2. In the figures hatchings represent those portions which were packed compactly with saw-dust particles. The structure of the nests of this species belongs to the branched pattern. never containing more than a single brood-cell in one branch-tunnel. Usually the entrance is slightly smaller than the tunnel, measuring 4–4.5 mm in diameter, while the tunnel is 5–6 mm. The brood-cell is somewhat larger than the tunnel, varying considerably in length. The preys are some species of large aphids belonging to the genus *Cinara* which is parasitic on Pinaceae, the winged form only rarely being involved. It seems of interest that the preys of the same genus are reported by Iwata in his observation carried out in Kyoto and district. The egg is subcylindrical in form, rounded at each end and slightly tapering posteriorly. In one instance it is 2.5×1.0 mm in dimension, wax-white in colour, with a shade of pale yellowish. The prepupa is cream yellow or yellowish white, never showing, during the larval period, the

Table 1. The nests of *Pemphredon japonicus* Matsumura.

Nest	Cell	Size of cell (mm)	Prey		Grub (mm)	Remarks	
			eaten	intact		concerning larva	concerning nest
L	1	11×6.0	?	8	10	Nearly full-grown	A completed nest. Examined on Oct. 10, 1946. The wasp was at work on Oct. 5.
	2	10×5.7	?	15	5		
	3	9×6.0	?	25	?	Unknown	
	4	10×5.8	?	28	?	Unknown	
M	1	11×5.6	—	30	egg	Near the middle of the cell.	An incomplete nest. Examined on Sept. 20, 1947.
	2	?×5.8	—	2	—		
K	1	8×5.6	2	10	5	Near the bottom	A completed nest (?). Examined on Oct. 20, when the wasp was resting in the burrow.
	2	11×5.7	8	4	7	Near the bottom	
	3	10×5.5	1	7	4	Near the middle	
	4	11×5.8	0	11	3	Near the middle	
	5	?×5.7	?	?	?	The cell was cut off	

vermilion tinge. The cocoon consists of a semitransparent layer of silken substance, smeared on the inner wall of the brood-chamber and, even after drying up, it can hardly be torn off from the cell. The data obtained from instances illustrated in the Figures are as shown in Table 1.

2. **Pemphredon (Pemphredon) pacificus** Gussakovskij

The form of the nest is shown in diagrams G, H, I, K, R, S, T, V and W of Figure 1. The pattern of structure is somewhat irregular as compared with that of *P. japonicus*. Cells were located sometimes aslant against the longitudinal tissue of the wood. A branch of the tunnel includes usually a single cell at the end. Sometimes, however, two or three cells are constructed in lineal arrangement. When burrowed in the standing tree, the main tunnel sometimes runs upward. The tunnel is 4–5 mm in diameter, slightly enlarged from place to place. The brood-chamber is either as broad as the tunel or slightly broader, with the length varying from 8 to 12 mm. The preys belonged to several species of small aphids; the greater part were *Anuraphis piricola* Okamoto et Takahashi, among the remainder being included *Macrosiphum gobonis* Matsumura, *Periphyllus* sp. and *Pterocomma* sp. Most of them were of the apterous form. The number stored in one cell varied greatly from one instance to another, according in the main to the size of the prey, showing 10–50 in general. Spare tunnels are found with a considerable frequency, always stuffed with saw-dust scratched from the wall of the gallery. The rate of provisionment varies considerably from individual to individual, being probably due either to the age of the insect or to the climatic conditions of the time. In Figure 3 is given an instance of observation which was done on Oct. 10, 1948. These wasps were nesting in the same trunk of a decayed tree and they were the owners of the nests shown by the corresponding symbols in Figure 1, excepting for D. The instance V may represent one of the most active cases of provisionment in this species. The time spent within the nest in each of her returns was as follows (sec.) : 30, 20, 15, 20, 18, 25, 30, 12, 15, 10, 20, 20 and 15. During the course of the above observation some attention was given to her mode of carrying the prey. The aphid was always seized by one end of its body with the jaws of the wasp. Its main part was held under her head, but by which end it was captured was not constant, although in most of the cases it was caught by the anterior end. However, it was always grasped from the back-side. The bodily orientation of the prey during the transportation would indicate the direction of attack by the hunter.

The egg is laid usually on one of the bottommost aphids, but cases there were wherein it was found on one located near the middle of the cell. It was similar in form and colour to that of the preceding species, the dimensions measured being as follows : 2.3×0.8, 2.3×0.7, 2.4×0.8 (mm). The manner of attachment of the egg to the pedestal pery is shown in diagrams J and U of Figure 1. The larva

of this species is provided with a pair of small tubercles on each of the segments 3–6, and sometimes it turns slightly reddish in colour after becoming the prepuppa. The cocoon is similar to that of *P. japonicus*.

This species is parasitized by *Ellampus punctatus* (Uchida), a species of small cuckoo wasps. The life of the parasite will be separately described later on.

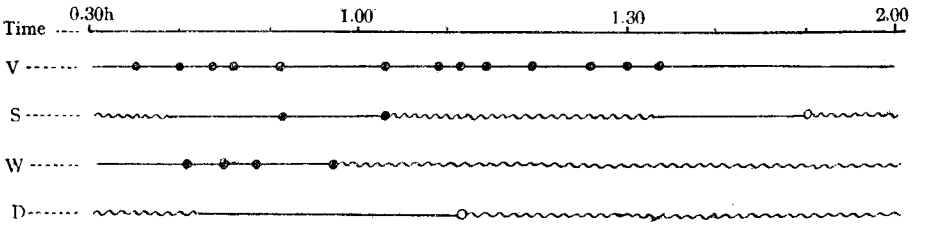

Fig. 3. Provisioning activities of four wasps of *P. pacificus* nesting in the same tree, from 0.30 to 2.00 p.m. The first three were the owners of the nests shown by the corresponding symbols in Figure 1. ● — to take in a prey ; ○ — to enter empty-handed ; solid line — to go out of the nest ; waved line — to stay in the nest.

3. **Pemphredon (Pemphredon) flavistigma** Thomson

On June 29, 1949, the writer found about 20 wasps of this species nesting in a big decayed tree standing in the Otane-valley of Jôzankei. Only one of the nests was burrowed within my reach. It was in the course of provisionment and had the structure shown in diagram F of Figure 1. Again in the same valley, on July 20, 1951, two nests were examined which were made in the hard tissue of a dead mulberry tree. One of the nests was burrowed from outside through an abandoned tunnel of some boring beetle larva, while the other from inside through the central hollow of the trunk. They were constructed side by side and their intricate branch-tunnels became somewhat entangled (Fig. 2, M). However, in no case did the tunnels touch the adjacent ones, although sometimes they were separated from each other by only a very thin wall. In the nest which was dug from outside, the wasp had been observed working on June 26, carrying out the debris from the tunnel. At the time of examination she was still at work. According to this instance it seems that the working periods of a wasp at her nest cover about a month or more.

The structure of the nests belongs to the branched linear type. But the lineal arrangement of cells does not always occur. Moreover, when it does occur, the number of cells included in a branch-tunnel does not surpass three, being usually only two. The tunnel is as large as the entrance of the nest, measuring 4.5–

5.7 mm in diameter. The portions of the brood-cells are not specially enlarged, varying from 6.5 to 14 mm in length. Partition walls between cells are also variable in thickness, ranging from 3 to 20 mm. The egg is 2.2–2.4 mm long, 0.5–0.6 mm wide and wax white in colour, almost entirely lacking the yellowish tinge. Its manner of attachment is shown in Fig. 4. Special attention should be

Fig. 4. Preys, an egg and two young larvae of *P. flavistigma*.

Table 2. A nest of *Pemphredon* (s. str.) *flavistigma* Thomson.

No. of cell	Size of cell	Thickness of tampon (mm)	No. of prey	Larva or egg	Remarks
1	12×5.0	4	22	3.0 mm	Larva on a 5th prey from the inside.
2	12×5.0	10	20	2.8	Larva on a 10th prey from the outside.
3	15×5.5	4	17	2.5	?
4	14×5.5	6	22	egg	Egg is on a 8th sphid from the outside.
5	—×5.5	—	8	—	In the course of provisionment.

paid to the position of the pedestal aphid in the cell as is given in Table 2. The number of preys stored in one cell varies from instance to instance, ranging from 8 to 22, mostly however being 15–20. All the preys are of the apterous form, belonging to a single unknwon species of the genus *Cinara*. The egg needs about 24 hours for hatching. The larva completes its growth in about 10 days and cocoons as usual, smaring a silky substance over the inner wall of the chamber.

Later, this cocoon turns brownish in colour. Development of the insect in the cocoon, however, ceases at this stage and the wasp hibernates in this prepupal state. Thus, the second generation of the spring wasp does not emerge in autums. This is a quite exceptional phenomenon among the members of the present genus. The larva in hibernation is golden yellow in colour, without showing a shade of varmilion.

From the cocoons that were placed in the laboratory eight adult wasps emerged at the end of April of the next year, of which seven belonged to the male. To my surprise, they were not the wasps that were hitherto accepted as the males of *P. flavistigma*. The fact requires to make some emendation concerning the combination of both sexes of some species of *Pemphredon*. Detailed accounts, however, will be given in another paper.

P. flavistigma is parasitized by a species of ruby-wasps (an underscibed species belonging to the genus *Ellampus* Spinola) which completes its growth early in summer and emerges in mid-summer of the same year.

4. **Pemphredon (Pemphredon) montanus** Dahlbom

On Sept. 29, 1947, numerous wasps of this species were observed working at burrowing or provisioning their nests on several decayed trees standing in a valley at Jôzankei. I captured one of the wasps at the moment of her emergence from the entrance of her nest, Strange to say, another wasp entered the same opening carrying a booty. So I captured her also when she came out of the orifice. To my surprise, however, the third wasp came back with an aphid and crept in from the same entrance. Again I caught and imprisoned her in a bottle. During the succeeding 5 minutes I could obtain two more wasps entering the same hole with a victim. I dug the trunk at once and found a comparatively large hollow running through the central axis of the wood. Probably the wasps had each her own nest at some divergent places within the cavity and were only utilizing the common entrance to the hollow[2]. The next year in June when I went to the place equipped with cutting tools, the tree had already fallen down and moistened heavily by the winter snow. I found only a single nest which could be imperfectly pursued. It was constructed after the manner of *flavistigma* and the larvae contained were all dead. Since this time several wasps of this species have been observed nesting. All the nests were burrowed in from inside of hollows of decayed trees and hence the entrance could not be found out.

5. **Pemphredon (Pemphredon) laeviceps** Gussakovskij

It has been observed that the wasps belonging to this species nested in

2) Similar habits were observed on *P. flavistigma* at Jôzankei on June 25, 1952. This time the number of wasps that were utilizing a single entrance in common attained as many as nine.

decayed wood of dead trees and carried in aphids as usually done by their congeners. But on account of the fact that their burrows were always dug so high beyond easy reach, details remain yet unknown.

6. **Pemphredon (Pemphredon) mandibularis** Tsuneki

Two instances of the nests of this species have been investigated up to now. One of them was nearly completed; it is illustrated in diagram A of Figure 1, while the other was at the beginning of the construction and is shown in diagram D of the same Figure. Nest A was examined on Oct. 8, 1946, in the course of its provisionment. The broad gallery situated just below the entrance hole was a deserted tunnel of some boring beetle larva wherefrom four branches were closely issued. Among them one was a spare tunnel, one was an empty pocket, probably the just-constructed 22nd cell, and the remaining two were the main tunnels which were again subdivided complicatedly. Of course, the nest belongs in structure to the branched lineal pattern. But the ratio occupied by the linearly arranged cells is not high. The data obtained from the nest are as shown in Table 3.

Three eggs and their manner of attachment are shown in diagrams B, C and E of Figure 1. They are 1.7–1.8 mm in length and 0.5–0.6 mm in width and pale yellow in colour. The larva of this species is markedly blackish in colour, much

Table 3. A nest of *Pemphredon* (s. str.) *mandibularis* Tsuneki.

No. of cell	Size of cell	No. of preys remained	Larva	Remarks
1	8×4.0	?	Prepupa	
2	12×3.5	27	8 (mm)	Nearly full-grown larva
3	11×3.5	?	7	
4	11×3.5	17	6.5	
5	13×3.5	20	5.0	
6	8×3.5	11	5.0	
7	8×3.5	15	5.0	
8	6×3.7	16	4.5	
9	7×3.5	25	5.0	
10	8×4.0	34	—	Preys were dried up.
11	9×3.5	38	—	Preys were dried up.
12	8×3.5	35	—	The egg was dried up.
13	6×3.5	36	—	The egg was dried up.
14	9×3.5	58	—	The egg was dried up.
15	?×3.5	?	?	
16	9×3.5	49	—	The egg did not hatch.
17	9×3.5	48	—	The same as above.
18	7×3.5	39	—	The same as above.
19	8×3.5	38	—	The same as above.
20	8×3.5	42	3.0	Just hatched larva.
21	10×3.5	41	Egg	
22	— 4.0	—	—	

more conspicuously so than in allied species ; probably this is due not only to the colour of the prey, but also to the structural character of its bodily wall. The prepupa is cream yellow, never showing any tinge of vermilion. Unfortunately all the larvae died during the course of breeding.

A second instance was observed on Sept. 20, 1947. A deserted tunnel of some boring beetle larva was utilized as the entrance gallery. The 1st brood-cell having the dimension of 10×6 mm was completed and 45 aphids were compactly assembled. On one of the bottommost preys an egg was stuck. The 2nd cell was at the beginning of provisionment, containing only 2 aphids. The victims belonged to an unknown species of the genus *Aphis*. They were purplish black in colour, measuring about 2 mm in length and all were of the wingless form. An instance of the provisioning activities of the wasps is shown in Figure 5.

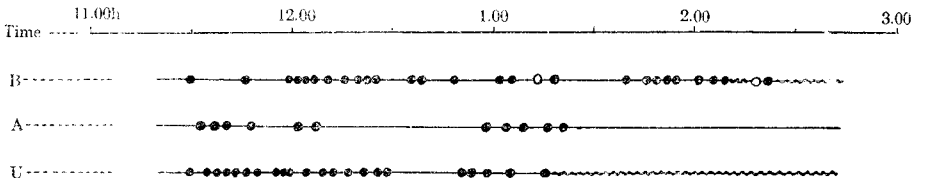

Fig. 5. Provisioning activities of three wasps of *Pemphredon*, nesting in the same tree. B — *P. unicolor*, the owner of nest B of Figure 2 ; A — *P. mandibularis*, the owner of nest A of Figure 1 ; U — *P. unicolor*.. Other symbols and lines are the same as in Figure 3.

7. **Pemphredon (Cerasophorus) intermedius** Tsuneki

So far as is known to me, this species seems to be parasitic on the nests of *Dinetus* spp. I have bred two male examples from a nest of *Dinetus unicolor* Panz. (shown in diagram B of Figure 2) and one male and four female examples from that of *D. shuckardi*. The nest of the latter instance was represented in diagram P of Figure 1, and its explanation will be given below in connection with *shuckardi*. When the nest was examined on July 12, 1947, each cell contained a larva. I reared them in a small glass tube, separating the cells with plugs of moistened cotten. On Oct. 20, all the larvae were in their respective cocoons which were composed of a thin layer of a pale yellowish sliky film smeared on the glass wall. Grains of cot were found excreted outside the cocoon. On the 29th of the same month, imagoes of *intermedius*, all female examples excepting No. 1, emerged from the cocoons. In this instance all the brood-cells of the host wasp were invaded by the parasite.

8. **Pemphredon (Dineurus) unicolor** Panzer

Nine nests were examined. They showed the structure as given in Figure 2, from A to J, excepting D. The nests belong to the multiple branched type, each branch containing a single brood-cell at the end. Only exceptionally 2 cells were arranged in a lineal order as indicated in diagram F of the same Figure. Spare tunnels were usually found in the nests. The tunnel varies slightly in width from one instance to another, measuring 3.0–4.0 mm in diameter. The brood-cell is hardly enlarged in comparison with the tunnel, but sometimes it appears more or less broadened. It varies greatly in length, ranging from 7 to 14 mm. The maximum number of cells made by a single wasp will be approximately represented by the instance B of the same Figure. In most cases, however, the wasp is supposed to make several nests of small scale during her life time. Instance A of the same figure is a case of the combined nests which will be a result of the work of at least two wasps. The portions shown by the crossed hatchings were stuffed very compactly with saw-dust particle mixed with numberless remains of aphids. In one brood-cell are stored usually 20–50 aphids, but sometimes the number attains as many as 60 or more, and sometimes, on the contrary, rests below 15, probably the difference depending in the main upon the size of the prey. Among the victims are included several species of aphids, the commonest one being *Aphis odinae* (Van der Goat). Two instances of provisioning activities of the wasps of this species were shown in Figure 5, one of which is concerned with nest B.

Table 4. Duration of the resting period and shift of coloration of the pre-imago stages of *Pemphredon unicolor* Panzer.

Cell \ Date	3	5	7	11	14	16	18	20	22	25
1	PP(dO)	PP(V)	P(dV)	P(dV)	P(lV)	P(lV)	P(Y)	P(B)	I(♀)	
2	fgL(Y)	PP(O)	PP(lV)	PP(dV)	PP(dV)	P(V)	P(lV)	P(O)	P(G)	I(♀)
3	fgL(Y)	PP(O)	PP(lV)	PP(dV)	P(dV)	P(lV)	P(O)	P(G)	I(♂)	

Abbreviation : PP..prepupa, P..pupa, I..imago, fgL..full-grown larva. Colour.. within parentheses : O..orange, V..vermilion, Y..yellow, G..grey, B..black, d..deep, l..light.

The egg is 1.7–1.8 mm in length and 0.5–0.6 mm in width, being always attached to the abdomen of the pedestal aphid by its cephalic end (Fig. 2, D). But the place of attachment is non-uniform either on the dorsal- or on the ventral side. Sometimes the egg is placed with its cephalic pole directed backward. The larva when it becomes prepupa, turns gradually vermilion in colour and remains in the state until beyond the pupation. The change of colour is very striking.

The lapse of time during the resting periods in the first generation (in June at Sapporo) as well as the shift in colour are given in Table 4, with regard to nest E. The cocoon is formed, as a rule, filling the space of the brood-cell, but it is not directly glued to the cell wall and hence can be taken out intact from the nest. It is simitransparent, pale yellow or pale brownish yellow in colour and is slightly enlarged toward the cephalic pole and flattened at the end. With a considerable frequency it is crowned with a cap-like accessory covering on top. Over the outer surface of the cocoon are attached usually remains of food and also grains of cot excreted, most abundantly so at the caudal end, viz. the lower end. The cocoon varies greatly in length, measuring 7–14 mm, in conformity with the length of the cell.

The nest of this wasp is parasitized by the species of small ruby-tailed wasps, *Ellampus auratus* (Linné). The same fact was also reported by some European investigators. From nest B, I bred 1 ♀ 2 ♂♂ of this brilliant cuckoo wasp, from nest C 1 ♂, from nest F 2 ♀♀ 3 ♂♂ and, from nest G 1 ♀. As to the larval habits of the parasites accounts will be given in another section.

9. **Pemphredon (Dineurus) lethifer fabricii** Müller

Three instances of nests were observed, each having been made in the pith cavity of dried reed-canes which were stood in a bundle along the outside of a cottage. One of the nests was made in the halm from below, while the others from above, containing 5, 2 and 3 larval cells respectively within the cavity. The brood-chambers were separated from the adjacent ones by the comparatively loose partition walls of saw-dust grains scratched off from the wall of the tube. The cells were 3 mm or so in diameter but varied in length from 6 to 10 mm. Victims provisioned were some unknown species of aphids. The number stored in one cell varied considerably from one cell to another, ranging from 28 to as many as 65. The egg was 1.2×0.5–1.3×0.6 mm in dimension, its shape, its coloration as well as the manner of its attachment being analogous to the case of allied species.

The wasp of this species does not use her sting in her hunting activeity. She approaches a flock of aphids at some moment when they are not guarded by ants and snatches off one of them, seizing it between her mandible. Then she flys up to alight on a nearbye leaf and gives a mere pressure to the aphid. After the operation the wasp carries it to her nest. The larval wasps do not become vermilion in colour during their prepupal stage.

In the material observed by me the partition walls between the cells were always present, althyugh sometimes they were very loose and thin. However, Ohgushi reported some interesting instances in which the separating walls were scarcely admittable, except few outermost ones. Hence numberless victimes were stuffed for a considerabte length in a tube as a mass, involving several youngs or

eggs at a certain interval. According to his observations cannibalism does not occur among the brood, and they form cocoons later in the lineal order in the cell. The nests are said to be found in dried halms of *Miscanthus sinensis* and in the pith of *Rubus palmatus*.

In Europe, the ethology of this species was best investigated among its congeners by several early authors. The wasp is said to nest in dried stems of elder trees and of common brambles, in the pith cavity of reed-canes as well as in the deserted holes of reed-galls of the small fly, *Lipara lucens* Meigen. As its parasite the brilliant cuckoo wasp, *Ellampus auratus* (Linné) is known.

10. **Pemphredon (Dineurus) shuckardi** A. Morawitz

Numerous nests of this species were found burrowed in the trunk of a dead tree. But I examined only 3 of them, one of which is illustrated in diagram P of Figure 1, to which allusion has already been made in connection with the ethology of *C. intermedius*. The other two were shown in diagrams O and Q of the same Figure. The tunnel of the nest was 2.5–3.0 mm in diameter and the larval cell is scarcely broadened as compared with the gallery, measuring 6–12 mm in length. The structure may be said to belong to the branched lineal type, but the occurrence of the lineal arrangement of the cells seems to be rather rare. The preys stored in one cell are 30–50 in number, chiefly belonging to a dark brown aphid species commonly found on shoots of *Sambucus buergeriana* Blume. In instance Q, the nest was in a stage soon after the beginning of construction. At the bottom of the tunnel were stored 7 aphids belonging to two unknown species, on none of which could be found the egg. Instance O was a completed nest, involving 7 cells within, of which E was an empty cavity, probably a spare tunnel. Contents of each cell had all become musty and were covered with moulds, containing either a dead larva or an unhatched egg. The wasps belonging to this species use their stings in hunting the preys. I observed frequently several wasps hunting on shoots of *Sambucus* trees. A wasp when she captures one of the aphids between her mandibles is used to rise on the wing. In the air, holding herself in stationary flight for a few seconds, she bends her abdomen quickly and darts her sting in a certain point of the ventral side of the prey. During hunting manoruvres, it was observed that the wasps feed themselves from time to time upon the aphids they catch, but in such a case they never sting the prey.

11. **Pemphredon (Dineurus) diervillae** Iwata

On the habits of this species a detailed record was published by Iwata. According to him the nests of this species are burrowed in fallen twigs of *Diervilla* or in wood of *Morus* logs. The structure of the nests belongs either to the simple branched type or to the branched lineal type, the latter occurring rather rarely. In one nest from several to 18 cells are involved, each being provisioned with aphids

(*Brachycolus* sp. and *Aphis* sp.), 15–39 in number, which are subjected to complete paralysis. The egg is laid on one of the preys in the same fashion as in allied species.

A single nest observed by the present writer at Sgpporo was made in a dead stem of *Aralia chinensis*, containing 4 cells which were arranged in a branched pattern. The nest was not yet completed. The preys belonged to one species of aphids (*Aphis* sp.) and were accumulated as many as 27-42 in number in one cell. The egg or the young larvae were found on the aphids located either at the bottom or near the middle of the cells. On Sept. 2, 1930, in Saitama Prefecture, the writer had an opportunity to observe the mode of hunting in this species. It was occurring on a young leaflet of *Quercus acutissima*. On the underside of the leaflet swarmed a flock of aphids which were the preys of the wasp. Always alighting on the upper surface of the leaflet when she came flying, the wasp went on foot at once to the preys beneath. There she gave one of the aphids 2 or 3 gentle strokes with the tip of her mandibles. The aphid pulled out its rostrum in amazement and attempted to escape. At that moment it was seized suddenly by the powerful jaws of the huntress and suffered a fatal sting on the underside of its body. Hunting was repeatedly carried out on the same leaflet. At last, she was captured by the writer and imprisoned in a tube bottle with the leaflet carrying the aphids. Inside the bottle, the wasp showed the manoeuvre of hunting in the same manner as she did in the open air.

On the larval habits of the cuckoo wasps, *Ellampus auratus* (Linne) and *E. punctatus* (Uchida)

The present writer has never had the chance of observation upon the parasitic manoeuvre of adult wasps of these small cuckoo wasps. But judging from the results of their activities, it seems probable that the invasion into a host's cell is carried out after the cell is completed or at some moment it is about to be completed, since the egg of the parasite is always found at some outer portion of the brood-chamber. However, the egg is never placed on top of the provisioned preys, but always concealed among them, either before or near the middle of the chamber. Probably the parasite, too, forces her way into the packed aphids and lays her egg on one of the preys which was located more or less apart from the outermost ones. The two species of parasites listed above appear to possess some measure of respective preference bearing upon the host species. This seems true. Because the writer has never secured *E. auratus* from the nests of any species of *Pemphredon* other than *unicolor*, and at the same time from several nests of *unicolor* he has bred several individuals of this cuckoo wasp. The same relationship is also the fact of *E. punctatus*. This species has been bred so far only from the nests of *P. pacificus*, so far as the genus *Pemphredon* is concerned. The larval lives of both species are much the same, so that the present account will be confined to a single instance that seems to

represent one of the most remarkable cases of their parasitism. It was found in a nest of *P. unicolor* which was illustrated in diagram F of Figure 2. This nest, when examined, was guarded by the mother wasp resting in the entrance gallery. Notwithstanding such care, out of 8 brood-cells found within, 6 were already invaded by the ruby-tailed wasp. From these 8 cells 7 larvae, 2 eggs and one dead egg were obtained. Among the larvae one that was found in cell No. 1 was a full-grown young of the Pemphredonid, two small ones feeding in cell No. 7 represented respectively a host and a parasite and the remaining four were all parasites, occupying cells No. 2, 3, 4 and 5, each in one cell. The fresh eggs were both placed in cell No. 8, and the dead one in cell No. 6. The larva of the parasite is very distinct in form by possessing a row of characteristic tubercles on the median line of the bodily segments as shown in diagram L of the same Figure.

In cell No. 7, both larvae were just hatched out. The host was situated near the bottom of the chamber, while the parasite near the entrance, each sucking the juice of the pedestal aphid. Both were similar in shape and size, but the host was much darker in colour, showing bluish black, while the parasite was brownish. They were placed in a cell of small glass tube, keeping the same relative position between them as in the natural cell. The next day when observed, the host was in the previous position of the cell, but it was mounted upon by the parasite and was being devoured by the latter. Possibly the parasite, after sucking up the pedestal aphid more quickly than the host, searched about for the rival through the packing of the victim to kill it. Thenceforth the parasite ate the aphids one after the other in the same fashion as the host, and finally spun the cocoon. The cocoon of the parasite consists of a semitransparent layer of silken substance smeared over the inner surface of the brood-cell. It was pale yellow

Table 5. The developmental process of the youngs of *Ellampus auratus* Linné (from July 22 to Aug. 16).

Cell \ Date	22	23	24	25	26	28	30	5	7	10	11	15	16
1	(Host larva)												
2	5.0	F	C	Died	—	—							
3	5.0	F	C	PP	PP	PP	P	B	G	I(♀)			
4	4.5	4.7	5.0	F	C	PP	PP	B	G	I(♀)			
5	4.0	4.5	4.7	F	C	PP	PP	B	B	G	I(♂)		
6	(Dead egg)												
7	3.0	K	4.0	5.0	F	C	PP	D	B	G	G	I	E(♀)
8	Egg	Egg	H	K	4.0	F	C	D	B	G	G	I(♀)	

Abbreviations: F..Full-grown larva, C..Cocooning, PP..Prepupa, P..Pupa, K..Killing the host, H..Hatching out, D..Becoming dark, B..Becoming blackish, G..Becoming greenish. I..Imago, E..Emerging from the cocoon.

in colour. In cell No. 8, the egg of the Pemphredonid was attached to one of the aphids located behind the middle of the chamber, while that of the cuckoo wasp was attached to the one placed before the middle, which was deposited quite in the same manner as was the host's egg. Subsequent process was much the same as that which occurred in cell No. 7. Developmental procedure of these parasites was as shown in Table 5. All the adult wasps transformed from these larvae belonged to *E. auratus*. Probably they were the brood of a single mother wasp which might be hiding in some corner of the tunnels during the course of the nesting activities of the Pemphredonid.

According to the recent investigations of Hymeno-pterologists it is said that the subgeneric name, *Cemonus* Panzer, 1806 (nec Jurine, 1801) should be adopted instead of *Dineurus* Westwood, 1837. In the present paper, however, the name, *Dineurus* was retained only for convenience' sake, since this is the continuance of the writer's pre-vious paper dealing with the classification of the genus *Pemphredon* in which the subgenus was represented as *Dineurus*; and it seems not desirable to alter the name of the same group of wasps within a series of the same treatise.

Literature

Adlerz, G. 1903. Lefnadsforhallanden och instinkter inom Familierna Pompilidae och Sphegidae. Svenska Vetenskapsak. Handl., XXXVII, N° 5, ref. p. 133.

————, 1906. Ibid., II, Vol. XLII, N° 1, ref. p. 37 et 40.

Berland, L. 1925. Faune da France, 10, Hymen. Vespif., I. ref. pp. 139-141.

Borris, H. 1897. Bidrag til danske Gravehvepses Biologi. Vid. Meddel. naturh. Kjobenhaven, ref. p. 84.

Brôngniart, Ch. 1890. (Note sur *Cemonus unicolor* Fabr.) Ann. Soc. entom. France, Bull, p. XCIII.

Chevalier, 1925. *Pemphredon lugubris* Latr. Hymènoptère manger du Pucerons. Bull. Soc. Sci. Seine-et Oise (2) 6, pp. 69-71.

————, 1926. (*Pemphredon lugubris* showing intelligence) Bull. Soc. Sic. Seine-et-Oise (2), 7, p. 83.

————, 1932. (*Cemonus unicolor* biology) Bull. Soc. Sci. Seine-et-Oise. Versailles (2) 13, pp. 24-27.

Curtis, J. 1862. British Entomology, Hymenoptera, n° 632.

Dufour, L. et Perris, E. 1840. Mèmoire sur les Insectes Hymènoptères qui nichent dans l'interieur des tiges sèches de la Ronce. Ann. Soc. entom. France, IX, ref. p. 36.

Giraud, J. 1863. Mèmoire sur les Insectes qui vivent sur le Roseau commun, *Phragmites communis* Tri. (*Arundo phragmites*) et plus spècialement sur ceux de l'ordre des Hymènoptères. Verh. z.-b. Ges. Wien, XIII, ref. pp. 1281-1282.

————, 1866. Mèmoire sur les Insecte qui habitent les tiges sèches du la Ronce. Ann. Soc. entom. France. ref. p. 471.

Goureau, 1855. (Note sur *Cemonus lethifer* et *unicolor* F.) Ann. Soc. entom. France (3), Bull., p. VII.

Iwata, K. 1937. Habits of four species of the Japanese hunting wasps that burrow in rotten wood. Mushi, Fukuoka, Vol. X, No. 2, ref. p. 136–138.

Kennedy, 1838. Observations upon the economy of several species of Hymenoptera found in a garden at Clampton. London and Edinburgh Philos. Magaz., XII, ref. p. 17.

Lepeletier, de S.-F. 1841. Histoire naturelle des Insectes Hymènoptères II, ref. p. 569.

Laboulbène, A. 1874. (Note sur *Cemonus unicolor* F.) Ann. Soc. entom. France, Bull. p. CXXVIII et CLII.

————, 1875. Note sur les dèjats causès aux tiges d'Eglantiers servant de porte-greffes, par le *Cemouns nuicolor*. Ann. Soc. entom France, pp. 303–304.

Lichtenstein, J. 1874. (Note sur *Cemonus unicolor* F. et *rugifer*) Ann. Soc. entom. France, Bull., p. CXXII.

Maneval, H. 1929. Notes sur quelques Hyménoptères. Ann. Soc. ent. France, 98, ref. pp. 290-291.

Micheli, L. 1930. Note biologische e morfologiche sugli Imenotteri. Mem. Soc. entom. ital., Genoa, IX, pp. 46–66.

Nielsen, J. C. 1900. Biologiske studier over Gravehvepse. Vidensk. Meddel. naturh. For. Kjobenhaven, ref. p. 272–273.

Ohgushi, R. 1950. On the biology of *Pemphredon lethifer fabricii* M. Müller (in Japanese). Shin-Konchu, Tokyo, Vol. 3, No. 11. pp. 10–11.

Pèrez, J. 1894. Notes zoologiques . Actes Soc. linn. Bordeaux, XLVII, ref. p. 232.

Schmidt, H. 1916. Einige biologische Notizen zu *Diphlebus unicolor* F. als Bewohner der von *Lipara lucens* erzeugten Schilfgallen. Zs. wiss. Insektenbiol., XII, S. 306-309.

Shuckard, W. E. 1838. A few observations upon the habits of the indigenous Aculeate Hymenoptera. Trans. entom. Soc. London, I, pp. 52–58.

Verhôff, C. 1891. Biologisch Aphorismen über einige Hymenopteren, Dipteren und Coleopteren. Ver. d. nat. Ver. preus. Rheinlande, Bonn, XLVIII, p. 8–18, ref. pp. 12, 15.