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Nests of Some Japanese Bumblebees (Hymenoptera, Apidae)

By

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(With 21 Text-figures and 17 Tables)

In the course of our bumblebee studies we have collected nests of various Japanese species. Unfortunately no precise records were taken for many of them. The present paper gives descriptions of some recorded nests. At recent advance of bumblebee studies, mere descriptions of nests might be thought already superfluous. Nevertheless, there are still many uncertain aspects even for the species in Europe and North America, where the studies have been made most intensively (Sakagami 1976). The bumblebee studies in Japan are still at an incipient stage and most previous descriptions of nests are incomplete. For example, *Bombus diversus* is one of the commonest species in Japan and the nests have been recorded several times. Yet before Katayama (1966a) no previous authors have accurately documented its feeding pockets built by larval cells, the presence or absence of which is one of the most important bionomic characters in bumblebees. At such situation it may be appropriate to give descriptions of some nests and related comments, in the hope of further advance of bumblebee studies in Japan.

Explanations

1) The adopted scientific names are those given by Sakagami and Ishikawa (1969, 1972; cf. also Sakagami 1976).

2) Nests are cited with abbreviations **SA-1** (=*B. schrencki albidopleuralis* Nest 1), **DD-A** (=*B. diversus diversus* Nest A), etc. The Arabic numbers refer to the nests studied by ourselves, and alphabets to those recorded by previous authors and cited in the text.

3) Unless specified dates are those of nest removal.

4) Terminology of bionomic characters follows Sakagami (1976). The term "batch" is defined as the group of immatures born in the same egg cell. Unfortunately this definition is exactly applied only to the cells where ovipositions were directly observed. For the cells the larvae in which spun cocoons and separated for each other, each batch can be distinguished only as the group of cocoons forming a cluster. By various reasons given in p. 132 the batches distinguished after cocoon spinning do not always correspond to real batches

defined above. The number of eggs laid by the queen in the same cell ranges usually 4～15, mostly 6～10, so that some batches containing more than 15 cocoons are probably composite ones. Further discussions are given in p. 132～135.

5) Each batch is designated as B 1 (n_1=number of immatures involved), B 2 (n_2), etc. from the nest bottom upwards. The sequence roughly but not exactly corresponds to the order of ovipositions. In some nests batches are divided in several groups according to the contents or assumed sequence and designated as 1a, 1b,.., 2a, 2b,.., or 1–1, 1–2, .. 2–1, 2–2, etc. "Mixed batches" mean those containing two or all of queen, worker and male immatures.

6) Abbreviations: *Q*, *q*=queen; *W*, *w*=worker; *M*, *m*=male. *C*=post-emergence vacated cocoon; *Ct*=those half torn and crushed, mainly located on or near nest bottom, fallen sideways or often filled with plant fibers (cf. Fig. 2, 0f/0g, 3a/3b; Fig. 7, 1–8, etc.); *Ci*=vacated but intact; *Cx*=empty but entirely or partly coated with wax, especially around the emergence hole; *Cy*=empty but the orifice provided with wax overgrowth (cf. Fig. 7, 2–23, 2–29). *H*=post-emergence cocoon with stored food; *Hh*=with honey; *Hhx*=with honey, coated with wax; *Hhy*=ditto, with wax overgrowth; *Hc*=with honey, coated with wax and orifice closed; *Hp*=with pollen. *A*=pre-emergence adult; *P*=pupa (*Po*=old, *Py*=young, white, eyes white to colored); *Pr*=prepupa, *Lo*, *Ly*=old and young larvae; *E*=egg; *d*=dead.

7) In most species queen cocoons are distinguished by their large size (measured by the maximum diameter) even after emergence. Distinction of male and worker cocoons is difficult after emergence or before pupation. Most cocoons shown without suffices *q*, *w*, *m* should have produced workers except those produced males in later colony stages.

8) The term "pot" is exclusively applied to entirely wax built ones, never to vacated cocoons used for food storage.

9) Various animals associated with nests were collected but these are not recorded in the present paper, except for some notes on the parasitism by *Mutila europaea mikado*.

Descriptions

Bombus (Thoracobombus) schrencki albidopleuralis (Skorikov) (=SA)

In Japan this form is confined to Hokkaido east of Ishikari depression and commoner in the eastern areas. Nakaguchi and Nishijima (1971) observed flight activities in a nest (**SA-A**). Two nests (**Ps/SA-A, B**) usurped by *B. pseudobaicalensis* were recorded by Sakagami and Nishijima (1973). All these three were surface nests built on the ground of a larch reforestation (Obihiro, Tokachi Prov.), with rich decaying plant matter. Two additional nests are recorded below, both taken in Akkeshi, Kushiro Prov., in 1958, by Mr. S. Maeda.

SA-1 (Fig. 1). August 3. On the ground surface of a fir reforestation. Outer cover 2.5 cm thick. Wax envelope absent. Nest mass about 4.5 cm in diameter.

Population: Adults Foundress + about 20 *W*. Cocoons 20 *Ct*·*i*+7 *H*+3*A* + 23 *Pyo*. (4 *d*) + 10 *Pr* (4 *d*)=63 (8 *d*). Pre-cocoons 1 *L* (1 cell) + 14 *E* (1 cell). Batch composition in Table 1.

Colony conditions: No cocoons were of queen size (cf. SA–2) and all pupae were *WW*. The nest have not produced sexuals. The numbers of adult *WW* and

Table 1. Batch composition in *B. schrencki albidopleuralis* Nest **SA-1**

Batch		Cocoon diameter (mm)					Contents
No.	Size	4	6	7	8	9	
1	7		3	4			7 *Ct*
2	10			6	3	1	6 *Ci*, 4 *Hh*
3	8	1	1	2	2	2	5 *Cx*, 3 *Hhx*
4	11			6	5		2 *Ci*, 3 *A*, 6 *Po* (1 *d*)
5	10		3	2	3	2	9 *Po*, 1 *Py*
6	10		4	3	3		2 *Po*, 2 *Py*, 3 *Pr*, 3 *Pd*
7	7		1	2			7 *Pr* (4 *d*)
8	1						1 *Lo*
9	14						14 *E*

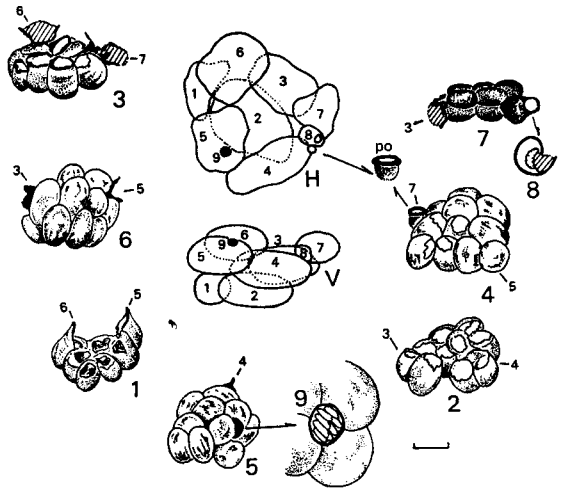

Fig. 1. *B. schrencki albidopleuralis* Nest **SA-1**. Horizontal and vertical views (H and V) of batch arrangement at center (In this and subsequent figures each batch is shown with Arabic No. as given in the text). Small Arabic No. in each batch represent connections with adjacent batches. Hatched=pollen deposit, po=empty storage pot. Scale for each batch =1 cm.

vacated cocoons do not much differ, suggesting a poor nest development after a late foundation. Only one larva in B 8 indicates elimination of other sibs.

Miscellaneous notes: B 1 half crushed and dislocated. B 2 at the center of nest bottom supporting other batches. Arrangement (Fig. 1, H, V) comparable to Type IV, *vogelnestartige Rosette* by Wagner (1907) and Weyrauch (1934). An unusually small, empty pot between B 4 and 7, and two amorphous pollen masses between B 3/6 and B 3/7, both only partly covered with wax. B 8 had a distinct

feeding pocket directing upward. Egg cell (B 9) built at a niche of pre-emergence cocoons of B 5, being flat, not primed with pollen. Eggs, probably queen born, laid horizontally and regularly.

SA-2 (Fig. 2). September 17. In a shallow depression on the ground of grassland admixed with shrubs. Outer cover of fine plant fibers and mosses 2 cm thick. Wax envelope absent.

Population: Adults Foundress+ 17 new *Q*+ 21 *W* captured. About 10 *W* escaped. Cocoons 181 *Ct.i*+ 22 *H*=203. No pre-cocoon immatures. Batch composition in Table 2.[1)]

Table 2. Batch composition in *B. schrencki albidopleuralis* Nest **SA-2**

Batch		Cocoon diameter (mm)							Contents
No.	Size	5	6	7	8	9	10	11	
0a	7		4	3					7 *Ct*
b	7		4	2	1				6 *Ct*, 1 *Cx*
c	7		2	5					7 *Ct*
d	5			3	2				5 *Ct*
e	7		3	3	1				7 *Ct*
f	8	1	2	4	1				8 *Ct*
g	8		4	4					8 *Ct*
1	14	3	4	7					14 *Ci*
2a	13		4	8	1				10 *Ci*, 3 *Cx*
b	10		2	4	2	1		1	2 *Ci*, 6 *Cx*, 2 *Hhx*
c	11			6	5				5 *Ci*, 5 *Cx*, 1 *Hhx*
3a	9			3	2	1	3		7 *Ci*, 2 *Cx*
b	9			3	1		2	3	9 *Ci*
4a	7			3	4				1 *Ci*, 4 *Cx*, 2 *Hp*
b	10		1	5	4				4 *Ci*, 2 *Cx*, 1 *Hh*, 3 *Hhx*
c	13			6	7				1 *Ci*, 8 *Cx*, 2 *Hpx*, 1 *Hhx*, 1 *Hc*
5	9	2	7						4 *Ci*, 1 *Cx*, 2 *Hh*, 1 *Hhpx**, 1 *Hc*
6	10				9	1			9 *Ci*, 1 *Cx*
7a	11					1	10		9 *Ci*, 1 *Cx*, 1 *Hp*
b	10					1	8	1	7 *Ci*, 1 *Cx*, 2 *Hpx*
c	9						9		5 *Ci*, 3 *Cx*, 1 *Hhx*
d	9						9		6 *Ci*, 2 *Cx*, 1 *Hpx*

* Honey admixed with pollen.

Colony conditions: Apparently at the end of brood production. It is likely but uncertain that no male was produced. Distribution of cocoon diameters shows production of small *WW* more in earlier stages. *QQ* were produced sporadically mixed with *WW* since B 2b. Judging from batch arrangement (Fig. 2), it is possible that B 3a, b were produced later than 4a~4c, but never after B 5. Mixed batches

1) In this nest and in the next two forms, batches are divided in some groups, probably corresponding to the order of ovipositions. The order among batches (a, b, ..) within each group is unknown.

are 2b, 3a, b (Fig. 2), and 6. Assuming the cocoons 10~11 mm wide as having produced *QQ*, the percentage ratio queen cocoons/total cocoons is 46/203 × 100 =22.6%.

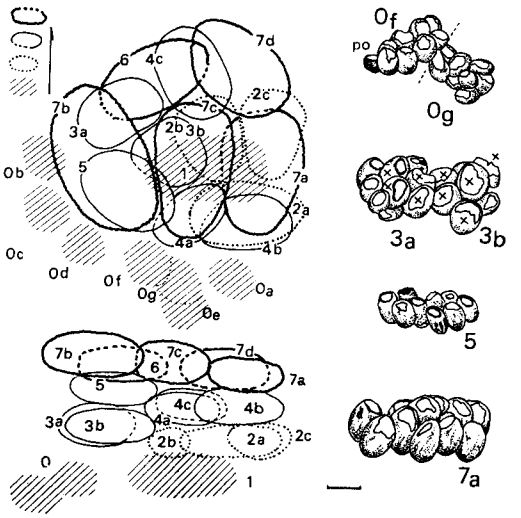

Fig. 2. *B. schrencki albidopleuralis* Nest **SA-2.** Left. Horizontal and vertical views of batch arrangement (In this and subsequent figures, vertical stratification of batches is shown by different contours, cf. left top). Right. Some batches. 0f/0g=all cocoons half torn, with an empty wax plot (po); 3a/3b=mixed batches (x=queens, other workers or males), all half torn; 5=consisting of typical dwarf cocoons; 7a=all queen cocoons. Scale=1 cm for all figures.

Miscellaneous notes: B 0a~0g were dislocated. The bottom of nest mass was occupied by B 1. Subsequent arrangement is atypically rosette like, skewed unilaterally, and the top is covered by large queen batches 7a~7d. Original rosette arrangement is traced by the empty space between 4a and 4c (Fig. 2). Yet, arrangement is intervened by dislocation of old batches, not being an outcome of simple upward growth.

Bombus (*Thoracobombus*) *pseudobaicalensis* Vogt (=Ps)

This species and the next form are confined to Hokkaido, where both are very common in lowlands, especially in open rural areas from which other forms are gradually retreating. More than a dozen of nests have been discovered by S.F.S., all on the ground surface, mostly of pastures, but few accurate records have been taken. Because two forms are isochromic and have not been distinguished until Tkalců (1962, cf. Sakagami and Ishikawa 1969), it is impossible to specify previous records. A nest described by Uchida (1934, as *Agrobombus gilvus*) should also be of either form. It was taken on August 10 from the surface of grassy area, involving the foundress, 16 *M* and 119 *W*. There were some large, probably queen

issuing cocoons. *Antherophagus nigricornis* was recorded as inquilinous beetle. One small nest is recorded below.

Ps-1 (Fig. 3). Misono, Kitami City, Kitami Prov., August 10, 1966 taken by Mr. Y. Ohé. On the ground surface of grassy area in a farm. Nest mass 5.5 cm in diameter. No further information. The nest was studied much later.

Population: Adults Foundress + 20 *W*. Cocoons 30 *C* + 50 *Ad*=80. Pre-cocoons Exact number unknown. Batch composition 1(7: 7 *Ct*), 2 (7: 7 *Ct*), 3a (14: 13 *Ci*, 1 *Ad*), 3b (11: 3 *Ci*, 8 *Ad*), 4 (7: 7 *Ad*). 5a (11: 11 *Ad*), 5b (11: 11 *Ad*), 5c (12: 12 *Ad*), 6～7 (larval cells), 8a～8c (egg cells).

Colony conditions: All cocoons were small and all dead adults were *WW*. Foundress was not much worn. Apparently still before producing sexuals.

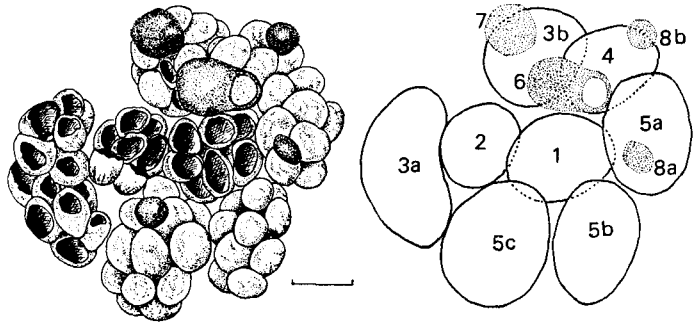

Fig. 3. *B. pseudobaicalensis* Nest **Ps-1**. Left. Horizontal view. Right. Ditto, batch arrangement. Scale=1 cm.

Miscellaneous notes: Batch arrangement like as in SA-1 around B 2, whereas B 1 dislocated. Egg cells are flat, built as in *B. schrencki*. B 6 had a distinct upward directing pocket while B 7 already not. Size distribution of adult females and age- and size-linked polyergism refer to pp. 136～142 (Figs. 15, 17, 18, Tables 14, 15).

Bombus (*Thoracobombus*) *deuteronymus deuteronymus* Schulz (=Dn)

A nest described by Sakagami (1951a as *B. senilis*) is of this form, which (**Dn-A**) was found on the ground surface of grassland (August 13, Kami-Oboro, Kushiro Prov.). Wax envelope absent. Adults No foundress +79 *W*+37 *M*. Cocoons 273. *Ct.i*+17 *A*+44 *P* (all *A* and *P*=*MM*)=334. Pre-cocoons 23 *L*+12 *E*. Nest is quite large for this species and taken after the death of the foundress and appearance of laying workers. No new queen was found. In the paper cited, this form was classified in non-pooket makers. This is erroneous as shown by the following record (Dn-1). A nest of *B. d. maruhanabachi*, a conspicuous subspecies in Honshu, was also found on the ground surface (cf. Sakagami and Ishikawa 1969).

Dn-1 (Fig. 4). Campus of Hokkaido University, Sapporo, August 3, 1976 by Mr. M. Ito and S.F.S. On the ground surface of a roadside covered with grasses 40

cm tall. Only mild attack at nest removal. Outer size incl. plant cover 13×12×10(h) cm and of nest mass 8×5.5×5(h) cm. Wax envelope absent. Most adults captured. Except larval and egg cells, nest was studied after emergence of all adults.

Population: Adults Foundress + 48 W at nest removal. Cocoons 59 *Cti.*+ 2*Hh*+58 *EM* (emerged till August 25, 29 *Q*+29*W*) +15 *d* (1 *Aw*+10 *Am*+ 2 *Aq* +2 *Pr*)=134. Pre-cocoons 15 *Lo*+27*Ly*+ 69 *E*=111. Composition of cocooned batches in Table 3, of precocoon batches B 11 (15 *Lo*), 12 (13 *Ly*), 13 (14 *Ly*), 14a (23 *E*), 14b (18 *E*), 14c (13 *E*), 14d (15 *E*).

Table 3. Batch composition in *B. deuteronymus deuteronymus* Nest **Dn-1**

Batch		Cocoon diameter (mm)						Contents (*EM*=Emerged after nest removal)
No.	Size	5	6	7	8	9	10	
0	4		2	2				4 *Ct*
1	6			6				6 *Ct*
2a	9			3	6			7 *Ct*, 2 *Hh*
b	8	1	1	2	4			7 *Ct*, 1 *Awd*
3a	9		2	4	3			9 *Ct*
b	10		2	4	1	3		8 *Ci*, 2 *Cx*
c	11		1	2	6	2		11 *Ci*
4	13		4	4	5			5 *Ci*, 8 *EM*
5a	5			1	4			4 *Amd*, 1 *Prd*
b	4			1	3			3 *Amd*, 1 *Prd*
6	10		1	2	3		4	10 *EM*
7	17		1	1	12		3	17 *EM*
8	10		1				9	10 *EM*
9	11						11	11 *EM*
10	7				3		4	2 *Aqd*, 3 *Amd*, 2 *EM*

Colony conditions: Colony attaining the stage producing sexuals. Most *WW* produced were still alive at nest removal (48 against 61 cocoons). Percentage ratio queen cocoons/total cocoons 23.1%. The number of produced *MM* seems low and their high mortality is noteworthy. B 6~10 were mixed batches and *WW* and *QQ* emerged with a considerable overlap:

Caste	Head width (mm)	Date (August)						
		~6	~9	~12	~14	~17	~22	~25
WW	2.8~2.9			1				1
	3.0~3.1		1					
	3.2~3.3					1		
	3.4~3.5		1					
	3.6~3.7	1	4	1	1	1		
	3.8~3.9	4	2		2	1		
	4.0~4.1	1	4	1				
	4.2~4.3	1						
QQ	4.4~4.5	2					1	1
	4.6~4.7		4	5	4	4	6	2

The number of eggs in B 14a~d, especially B 14a, was high and might possibly be worker born, though eggs were laid regularly, not irregularly as by laying workers of some *Bombus* s. str. species and *B. d. diversus* (E. K., unpubl.).

Miscellaneous notes: Batch arrangement can be called two storeyed rosettes. B 2a~5b form a rosette on B 1. B 6 fills the center and supports the later batches. B 1 and B 6 are separated by a space (Fig. 4, V). Egg cells are flat and somewhat elongate (l×w×h (mm): B 14c 10×5×4, 14d 6×3×2), built at niches between pre-emergence cocoons, and not primed with pollen. Feeding pocket (Fig. 4) was

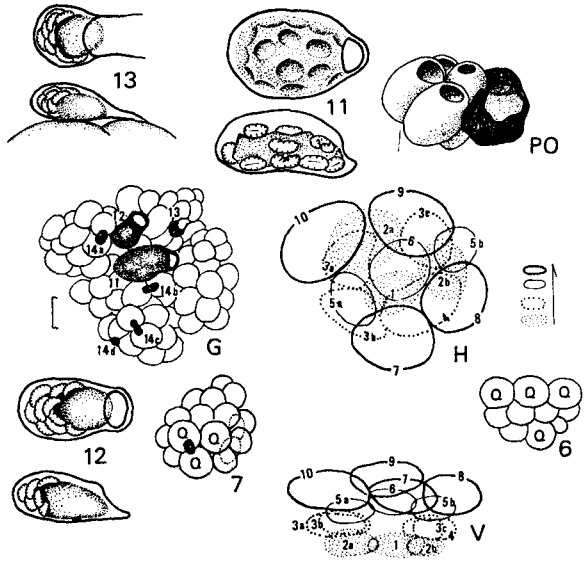

Fig. 4. *B. deuteronymus deuteronymus* Nest **Dn-1.** G. Horizontal view. H and V. Horizontal and vertical views of batch arrangement (Scale=1 cm). Some batches shown with Arabic No., dotted=pollen mass, Q=queen cocoons. Three larval cells, 11~13, showing interior. po=pollen pot.

rudimentary in B 13, well developed and rather directing laterally in B 12, similar but smaller in B 11. All 3 larval dells were provided with plentiful pollen mass. In B 11, larvae lay each in a shallow depression on the surface of pollen mass (cf. Fig. 4). A honey pot and a pollen pot (Fig. 4, Po, 16 mm wide, 12 mm long) were found at nest periphery. Cocoons pale yellow and wax dark brown. From batch arrangement, it is certain that *QQ*, and probably *MM*, too, were fed through pockets, not directly through cell walls as in some *Fervidobombus* (Hobbs 1966a, cf. Sakagami 1976, p. 408). Size distribution of females and age- and size-linked worker polyergism refer to pp. 136~142 (Figs. 15, 17, 18, Tables 14, 15).

Bombus (*Diversobombus*) *diversus diversus* Smith (=DD)

This form is one of the commonest bumblebees in Honshu, Shikoku and Kyushu, inhabiting from lowlands to low mountainous areas. First, previous nest records are summarized:

Abe (1932). **DD-A**. Ogino, Yamagata Pref., Nov. 11. In the hollow of a chestnut stump. No attack at nest removal. Batch size 8~23, mostly 12~16. Cylindrical honey pot present. About 1/3 of cocoons infested by *Mutila europaea mikado*.

Katano (1948). **DD-B**. Usune-Mura, Gumma Pref., June 25. In a mole burrow in a bamboo bush, about 20~30 cm deep, canal 60 cm long. Foundress + ca. 80 *W*. Early stage nest.

Morimoto et al. (1951). **DD-C**. Funatani, Hyogo Pref., June 8. In a burrow of small mammal in forest. **DD-D**. Funatani, October 28. In a mouse tunnel in a paddy field ridge, about 10 cm deep, canal 1 m long. No attack at removal. Wax envelope present. Adults 12 new *Q*+150 *W*+15 *M*. Cocoons 154 *Ct.i*+55 *Cx*+102 *Hh*=311 (102 *Cq*). Pre-cocoons 2 larval cells, one with 10 *L* and 2 "pollen bowls" (=feeding pockets), another smaller with a pollen bowl (=pocket). **DD-E**. Mt. Hikosan, Fukuoka. Under a stone 20 cm deep.

Miyamoto (1959). **DD-F**. Sasayama, Hyogo Pref., September 28. In an underground cavity 50 cm deep, canal 1 m long. Foundress + 16 *W*. Cocoons 438, some large, probably *QQ*.

Miyamoto (1960). Sasayama. Three nests recorded without detailed information.

Katayama (1965, '66a, b). Observations of oviposition behavior and colony development with 3 nests (A, B, C) as referred to below.

Tsuneki (1970). **DD-G**. Locality unmentioned, August 20. In an underground cavity of small mammal. No attack at nest removal. About 80 adults with foundress. "Pollen pot" by larval cells (=feeding pockets). Larvae 10~15 per cell, eggs 12 and 16 in 2 cells each. **DD-H**. Mitsudani, Fukui Pref., August 17. In a basket half filled with charcoal and put in a dark corner of the upstair of a small pen. 43 *C* (4 batches, respectively 10, 12, 12, 9), one batch with 12 *P*, and a cell with 12 *L*. **DD-I**. Fukui City, October 23. In a snake's brood chamber, canal 50 cm long. About 10 adults, some ones as large as *Q*. Nest in decomposition, leaving 2 intact batches (12 *C* and 7 *P*, probably *WW*). **DD-J**. Arashi-Mura, 800 m, Fukui Pref., June 27. In an underground cavity 60 cm deep, canal 70 cm. long. Contents 13 *C*, 7 *Pr*, 10 *L*. Pollen pot (=feeding pocket) attaching to the larval cell.

Matsuura et al. (1970). Kibi, Wakayama Pref. Many nests seem to produce no *QQ*. Two cases, **DD-K** August 24. Dead foundress + 40 *W*. No *Q* production to October. **DD-L**. October 18. Foundress + 20 *W*. No *Q* production.

Among the following records, Nest **DD-10~12** were collected by Mr. K. Fukushima in Shimojô-Mura, Nagano Pref. and sent to S.F.S. All others were taken by E.K. in Tochigi Pref., unless mentioned, in Tanohara, Yaita City.

DD-1. Late July, 1951. In an underground cavity (35 cm deep) in a mixed forest 4~5 m high. Foundress + ca. 110 *W*. Cocoons ca. 400. Many egg and larval cells. Still before queen production.

DD-2. Mid July, 1953. In an underground cavity (30 cm deep) in a *Cryptomeria* reforestation. Foundress + ca. 70 *W*. Cocoons ca. 280. Many egg and larval cells. Still before queen production. Reared but perished after one month.

DD-3. Early May, 1954. In a thick deposit of fallen leaves in a bamboo thicket. Foundress + 3 *W*. The first batch (ca. 10 cocoons) alone. Reared but the queen disappeared.

DD-4. Late June, 1954. In an underground cavity (15 cm deep) in a sloped *Miscanthes* grassland. Foundress + ca. 60 *W*. Cocoons ca. 180. Many egg and larval cells. Still before queen production.

DD-5. August 21, 1960. In an underground cavity (30 cm deep) in a *Cryptomeria* reforestation. No foundress + ca. 80 *W*. Cocoons ca. 450. Few egg and larval cells. No queen production. Many ♂♀ of *Mutila europaea mikado* in nest. Reared but issued only *Mutila*.

DD-6 (=Colony C in Katayama 1966b). Nikko, August 14, 1962. In an underground cavity (30 cm deep) between tree roots in a *Cryptomeria* forest 15~20 m high. Entrance of canal camouflaged (cf. Sakagami 1976, p. 396) with piled leaves. Outer cover poor. Wax envelope only partial. Foundress + 130~140 *W*. Cocoons 274 (10 post-emergence batches, 6 pre-emergence ones), larval cells 11 and egg cells 5. Still before queen production. One *Mutila* ♀ is laying many eggs. There are found *Mutila* eggs on the body surface of host prepupae removed from cocoons.

DD-7 (=Colony B in Katayama 1965 and Colony D in 1966b). July 21, 1963. In an underground cavity (30 cm deep) in a westerly facing slope, canal about 50 cm long. Foundress + 18 *W*. Cocoons 53 (3 post-emergence batches, mostly *Hh*, and 2 pre-emergence ones), larval cells 3, egg cells 2. Reared and produced 165 cocoons till September 18. No *Q* production.

DD-8 (=Colony C in Katayama 1965, and Colony E in 1966b). May 16, 1964. In an underground cavity (21 cm deep) in a *Cryptomeria* reforestation 2.5~3 m high, canal 50 cm long. Foundress + 7 *W* and 19 cocoons at nest removal. Reared and produced 338 cocoons till October 27, issuing no *Q* and 66 *M*.

DD-9. Late September, 1951. In an underground cavity in a chestnut forest. Not excavated. A large nest with 200~300 foragers, possibly with 800~900 adults and 1,500 cocoons.

DD-10. September. Underground nest, broken during transport.

Population: Adults unknown, only foundress and 3 *W* sent. Cocoons 76 *C* +1 *Pd*+ 7 *Pr*+1 *Mutila* ♂ =85. Batch composition (the order only an approximation): B 1~5 (all *Ct* an 7~8 mm in diameter) 1(8), 2(7), 3(7), 4(7), 5(9), 6(9 *Ci*, 8~9 mm), 7(7: 5 *Ci*, 1 *Cx*, 1 *Mutila* ♂), 8(9 *Ct*, 9 mm), 9(6 *Ct*, 9~10 mm), 10 (8 *Ct*; 7, 10 mm; 1, 7 mm); 11(8: 1 *Pd*, 7 *Pr*, with vestige of a feeding pocket). A poor nest not producing *QQ*. According to the collector, the bees were indifferent to many *Mutila* walking in the nest.

DD-11. September. Underground nest broken during transport. Heavily infested by *Mutila*.

Population: Adults unknown. Cocoons 100 (11 batches), all 8~7 mm wide, e.g. non-*Q* ones. No pre-cocoon cell. Batch composition in Table 4 (the order only an approximation).

Table 4. Batch composition in *B. diversus diversus* Nest **DD-11**

Batch		Cocoons issuing							
		Bees			*Mutila*				
No.	Size	Post-emergence	Prepupa	Larva (dead)	Post-emergence	Adult ♀	Adult ♂	Pupa ♀	Larva
1	14				14				
2	9				7	1		1	
3	11	4			6			1	
4	12	3			4			5	
5	9	2			2	5			
6	7				4		1	2	
7	11	3		(1)	2			5	
8	6	3				1		2	
9	10		1		5			3	1
10	8	1			2			5	
11	3			3					

Miscellaneous notes: The cocoons issuing *Mutila* are easily distinguished by a small circular hole at the top and the inner wall lined by parasite cocoon. Percentage ratio of infestation attained 79%, with a distinct proterandry. That no batches escaped the infestation by *Mutila* shows very early invasion of *Mutila* into the nest, perhaps when the first batch transformed to cocoons. Some cocoons were smeared with wax. A large empty pot by B 3. Table 4 shows that B 2 was also solitarily reared by the queen as no worker emerged from B 1.

DD-12 (Fig. 5). October 3. In an underground vole burrow in a sandy and moist ground, densely covered with dead leaves. Dark brown and brittle wax envelope covering most part of nest top, connected by means of pillars 0.3~0.5 mm thick (Fig. 5). Nest mass 12×15×8(h) cm.

Population: Adults unknown. Cocoons 451 *C* (373 *Ct.i*+64 *Cx*+2 *Hh*+12 *Ct.i.q*)+ 21 *A* (7 *Am*+14 *Aq*)+15 *P* (13 *Poq*+1 *Pyq*+1 *Pqd*)+2 *Pr* (1 *Pr*+1 *Prq*) =489. Pre-cocoons 5 *L*. Batches, 51 in total, were divided into 5 groups and the composition is given in Table 5. B 1-*n* may be older on the average but not necessarily than B 2-*n*.

Colony conditions: At the climax of colony development. Most *QQ* were produced from mixed batches (12 against only 2 pure *Q* batches). Percentage ratio of queen cocoons/total cocoons=8.4%.

Miscellaneous notes (Fig. 5): 1) Stored honey very scanty, only 2 *Hh*. Many of *Cx* (64 in total) should be used once for honey storage. 2) Two empty pots by B 3–6 and B 3–8. 3) The presence of pockets by B 5–1 and 5–2/3 indicates feeding of sexuals through pockets. These pockets and cell interior were separated by wax wall as in **DT-1**. 4) The pocket of B 5–1 with 3 *L* already separated one another with flimsy silken nets was abnormal in position, e.g. made at the center of

Table 5. Batch composition in *B. diversus diversus* Nest **DD-12**
(*=mixed batch, Q=queen batch)

Batch			Cocoon diameter mm (number)	Contents
Group	No.	Size		
1 (not wax-coated)	1	7	6~7 mm	B 1~17 all *Ct*
	2	11	〃	
	3	11	〃	
	4	8	7	
	5	12	〃	
	6	11	〃	
	7	12	7(11), 8(1)	
	8	11	7~8	
	9	12	6(1), 7(11)	
	10	11	7~8	
	11	9	8~9	
	12	13	〃	
	13	8	〃	
	14	6	〃	
	15	11	〃	
	16	12	〃	
	17	14	〃	
	18	12	〃	11 *Ct*, 1 *Cx*
	19	12	6(1), 9(11)	B 19~26 all *Ct*
	20	13	9	
	21	13	6(9), 7(4)	
	22	11	9	
	23	11	9~10	
	24	13	〃	
	25	12	10	
	26*	7	8~9(5), 13(2)	
2 (more or less wax coated)	1	8	9	7 *Ci*, 1 *Cy*
	2	17	7(1), 8(16)	15 *Ci*, 2 *Cx*
	3*	6	10(2), 12~13(4)	5 *Ci*, 1 *Cx*
	4	18	7(2), 9~10(16)	16 *Ci*, 2 *Cx*
	5	16	9~10	14 *Cx*, 2 *Hc*
	6	9	〃	1 *Ci*, 8 *Cx*
	7	5	9	5 *Cx*
	8	7	9~10	7 *Cx*
	9	10	9(4), 13(6)	8 *Ci*, 2 *Cx*
	10	6	9~10	2 *Ct*, 4 *Cx*
	11	9	10	9 *Cx*
	12*	6	10(4), 13(2)	6 *Cx*
3 (partly pre-emergence)	1Q	6	12~13	2 *Ciq*, 4 *Aq*
	2*	8	10(1), 13(7)	1 *Ciq*, 6 *Aq*, 1 *Am*
	3*	9	9(5), 13(4)	5 *Ci*, 2 *Ciq*, 1 *Aq*, 1 *Poq*
	4*	12	9(11), 13(1)	1 *Ciq*, 10 *Ci*, 1 *Am*
	5*	13	9~10(9), 13(4)	6 *Ci*, 1 *Aq*, 2 *Am*, 3 *Poq*, 1 *Pr* (Fig. 5)
	6*	9	8(3), 13(5)	7 *Ci*, 1 *Cx*, 1 *Aq* (Fig. 5)
	7*	8	9(5), 13(3)	4 *Ci*, 1 *Cx*, 1 *Aq*, 2 *Poq*
	8*	8	8(2), 9(2), 13(4)	1 *Ci*, 1 *Ciq*, 3 *Am*, 3 *Poq*
4 (no adults)	1*	7	10(4), 13(3)	4 *Ci*, 2 *Ciq*, 1 *Poq*
	2Q	9	13	3 *Ciq*, 3 *Poq*, 1 *Poq*, 1 *Pyq*, 1 *Pdq*, 1 *Prq*
5 (larval cell)	1	3		3 *Lo*
	2	1		1 *Lo*
	3	1		1 *Lo*

the cell. 5) B 5–2/3 had a common pocket (cf. Sakagami et al. 1967). The presence of only one larva in each cell suggests deaths of other larvae and subsequent elimination by workers. 6) As a whole cocoon diameter tended to increase in parallel with nest development.

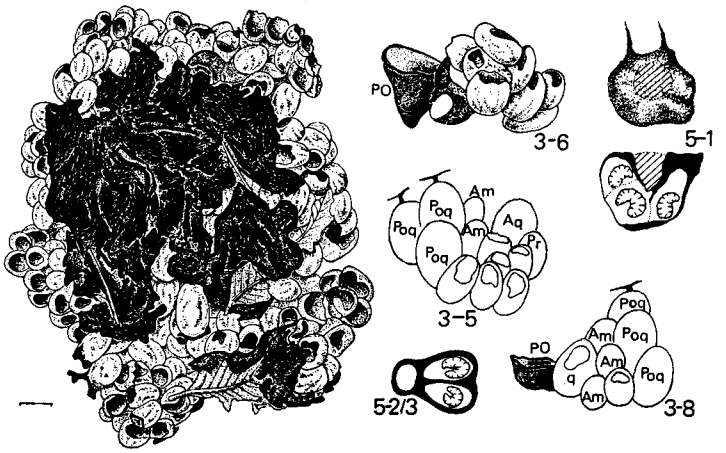

Fig. 5. *B. diversus diversus* Nest **DD-12**. Left. Horizontal view (with wax envelope), Scale=1 cm. Right. Some batches shown with Arabic No. 3–6=mostly torn, with an empty wax pot; 3–5/3–8=mixed batches, Po=old pupa, Pr=prepupa, A=adult, q, m =queen and male, 3–8 with an empty wax pot; 5–2/3=two larval cells, each containing only one larva, with common feeding pocket; 5–1=three larvae with abnormally placed pocket (hatched=pollen).

DD-13. Amayu, Shiobara, 650 m, September 5, 1976. In an underground cavity in a *Cryptomeria* reforestation. Entrance hole 5.5×2 cm, surrounded by a pile of black soil removed by workers from the interior. Canal about 2.5 cm wide, the first section (7 cm) subhorizontal, then bending more vertically. Nest cavity 20 cm below surface and 13×16 cm in extent. Nest mass covered with fine pieces of *Cryptomeria* bark, leaves of chestnut and oaks, and mosses, admixed with some torn pieces of cocoons. Both cavity and plant matter for the nest cover are those used by some small mammal. Wax envelope virtually absent.

Population: Adults Foundress + 174 *W* collected, ca. 20 foragers escaped, no dead *Q* and 3 *Wd* on nest bottom. Cocoons 761 *C*+ 99 *P* or *Pr* (7 *d*)=860. Pre-cocoons 9 larval cells + 3 egg cells.

Composition of cocooned batches: B 1~54 mostly consisting of *Ct* or *Ci*. The lowest BB, 1~12 infested by mold and wax moth larvae. B 1 (12, probably the real first batch), 2(13), 3(10), 4(10), 5(13), 6(14), 7(10), 8(14), 9(14), 10(8), 11(17), 12(15), 13(7), 14(12), 15(18), 16(16), 17(14), 18(12), 19(13), 20(16), 21(17: 16 *Ci*, 1 *P*), 22(17), 23(15), 24(20), 25(20), 26(18), 27(14), 28(13), 29 (16: 15 *Ci*, 1 *Pd*), 30(16), 31(18), 32(16), 33(17), 34(17), 35(17), 36 (20), 37(18), 38(19), 39(19), 40 (19), 41(13), 42 (16: some *Hh*), 43(14), 44 (18: some *Hh*), 45(14), 46 (17: some *Hh*), 47 (15: some *Hh*), 48 (10: 9 *Ci*, 1 *P*), 49 (15: 10 *Ci*, 5 *P*), 50 (13: 8 *Ci*, 5 *P*),

51 (11: 6 *Ci*, 5 *P*), 52 (18: 7 *Ci*, 11 *P*), 53 (16: 4 *Ci*, 12 *P*), 54 (20: 4 *Ci*, 16 *P*), 55 (10 *P*), 56 (6 *P*), 57 (13: 9 *P*, 4 *Prd*), 58(7: 6 *P*, 1 *Prd*), 59(3 *Pr*), 60 (3 *Pr*), and 4 dislocated *Ci*.

Colony conditions: The largest nest of *B. d. diversus* hitherto precisely documented, though no *Q* production was seen at nest removal. Batch composition is characterized by numerous empty cocoons, few pupae and prepupae, and relatively many young immatures. Perhaps laying activity of the foundress once dropped about 10～15 days before nest removal as suggested by small size of B 56～60.

Later production by laying workers: The nest was transferred in an observation box. The foundress died at transfer. Cocoons and pre-cocoon batches built before transfer produced respectively 86 *W* and 14 *M* (2 *Pd*) but no *Q*. These cells might have been built either by the foundress or by laying workers. The dropped queen productivity mentioned above favors the latter assumption. After transfer in the box laying workers produced the following batches, though the number of eggs laid by workers was much larger than those of immatures spun cocoons:

1(1), 2(2), 3(5), 4(2), 5(5), 6(6), 7(4), 8(1), 9(1), 10(2), 11(4), 12(1), 13(2), 14(5), 15(3), 16(3), 17(7), 18(1), 19(1), 20(1), 21(4), 22(1 *Pd*), 23 (11: 10+1 *Pd*), 24(7), 25(1).

Batch size is distinctly smaller than in queen born batches. Until October 29 938 adults (847 *W* + 91 *M*) emerged from the nest and total cocoon production amounted to 949 (854 *W*+ 95 *M*). Additional notes on the behavior of laying workers will be described elsewhere.

Miscellaneous notes: Some remarks on nest structure are enumerated (*= those more or less common to other nests). 1)* Both queen and worker built egg cells not primed with pollen. 2)* Egg cells built on spinning and post-spinning cocoons, mostly isolately. Workers built cells on other places as well as on cocoons, either isolatly or in group. 3) Orientation of worker laid eggs irregular in many cells. 4)* Larval cells with distinct upwards directing pockets. Frequently more than one pocket formed. 5) Size of most batches produced from queen built cells very large as in DT-1. 6)* Admixing torn pieces of old cocoons into the nest envelope. 7) * Nest mass very loose, not compact as in *B. ardens*.

Bombus (*Diversobombus*) *diversas tersatus* Smith (=DT)

Tsuneki (1970) recorded an above-ground nest of this form from Jôzankei in Sapporo (September 10, 1945): "The bees enter a hollow that had the entrance on the trunk of a dead tree still standing .... The place was a flooded marsh and I could not go to the tree. The tree was rotten .., it was about 30 cm in diameter and the hole was open about 3 m above the water." Many bumblebee species are fairly plastic in nest site preference, and above-ground nesting seems not so rare as formerly conceived (cf. K.W. Richards 1975, Sakagami 1976, p. 394). But the above record cannot be regarded as authentic, because another isochromic form, *B.* (*Thoracobombus*) *honshuensis tkalcui* occurs in the same area, and the both cannot be distinguished in the field. One of us (S.F.S.) found traffic of *B. d. tersatus* at the holes on the ground surface 4 times but the nests were not excavated. A large nest excavated by Nishijima (pers. comm.) in Obihiro was subterranean. Two nests are recorded below.

DT-1 (Fig. 7). Botanical Garden, Hokkaido University, Sapporo, September 8, 1960, taken by Dr. K. Moriya and S.F.S. Built below a corner stone of a wooden hut destined to removal (Fig. 6, **DT-1**). Traffic of bees found at a narrow slit of wooden basement. Slit and nest cavity separated by an ample underfloor space (1.6 m distant for each other). Nest canal not well defined but the mainly used course marked with plant fibers scattering here and there. Nest cavity 30×

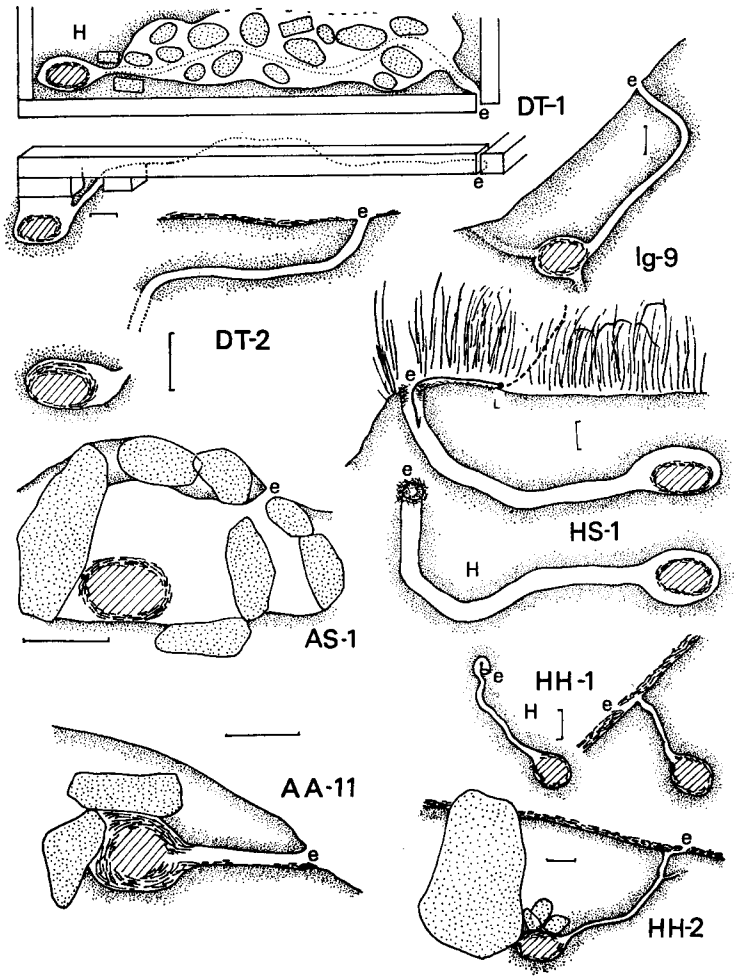

Fig. 6. Sites of some underground nests. H=horizontal view, all others=lateral view, e=entrance of nest canal, dotted=stone, hatched=nest mass, scale=10 cm. **DT-1, 2** *B. diversus tersatus*; **Ig-9** *B. ignitus*; **AS-1** *B. ardens sakagamii*; **AA-11** *B. ardens ardens*; **HS-1** *B. hypocrita sapporoensis* (L=alighting point); **HH-1, 2** *B. h. hypocrita.*

25 cm and its bottom 29 cm below the stone. Outer cover consisting of dead leaves and materials used by rat, pieces of vinyl sheets, packing paper, cloth, etc. Inner wax envelope dark brown, entirely covering nest mass (15×12 cm). Nest was removed after capturing foragers separately. No attack was exhibited but many house bees took the upside down defensive posture characteristic to bumblebees.

Population: Adults 2 new *Q*+ 121 *W* +20 *M*, with foundress + 5 *W* + 3 *M* dead in nest. Cocoons 637 *C* (176 *Hh*)+4 *d* (3 *L*+1 *Aw*) +13 *Am*+120 *Pm*+61 *Pr*=835. Pre-cocoons 31 *L* (9 cells) and 134 *E* (25 cells). Some eggs (cf. B 8–19/21, below) and larvae (cf. B 7–1/2) were possibly eliminated or lost at or before nest removal. Batches were classified in 8 groups: 1. Post-emergence cocoons, mostly *Ct*. 2. Ditto, mostly *Ci*. 3. Some cocoons with *AA*. 4. Some cocoons with *Po*. 5. Some cocoons with *Py*. 6. *Pr*. 7. Pocketed cells. 8. Egg cells. Batch composition of groups 1∼4 in Table 6 and of groups 5∼8 as follows. Groups 5∼6 (level/size/contents): 5–1 (3/7/6 *Pym*, 1 *Pr*), 5–2 (4/6 *Pym*), 5–3 (3/8 *Pym*), 5–4 (4/6 *Pym*), 5–5 (3/8 *Pym*), 5–6 (3/4 *Pym*), 5–7(3/7 *Pym*), 5–8 (4/8 *Pym*), 5–9 (5/6 *Pym*), 5–10 (4/10/6 *Pym*, 1 *Pr*), 5–11 (4/7 *Pym*), 6–1 (5/6), 6–2 (4/8), 6–3 (4/5), 6–4 (4/6), 6–5 (3/7), 6–6(3/5), 6–7(3/4), 6–8(3/12), 6–9(5/6). Group 7: 7–1(0), 2(2), 3*(7) (*=cf. Fig. 7), 4*(4), 5*(4), 6(5), 7(1+), 8(4), 9(4). Group 8: 8–1 (6), 8–2/3/4(9/7/5), 5/6*(6 *Ly*/5), 7/8/9* (9/5/5), 10(6), 11/12/13*(5/7/9), 14/15*(8/8), 16/17/18(6/6/2), 19/20(0/0), 21(1+), 22/23/24/25* (7 *Ly*/3 *Ly*/4/5). Relation between these groups and levels in the nest mass is:

	No. batches in level				
Group	1	2	3	4	5
1	10	5	1		
2	11	10	7	1	
3		2	2		
4		1	4		
5			5	5	1
6			4	3	2

Colony conditions: At the climax. Foundress died after producing one *Q* batch (2–18, cf. Fig. 7). 14 new *QQ* emerged and two stayed at nest removal. Laying workers produced most if not all *M* batches. Percentage ratio queen cocoons/total cocoons (14/835)=1.7%, or 14/645=2.2% if subtracting probable contribution by laying workers.

Batch arrangement: Batches occupying higher levels are more numerous at nest periphery, indicating a slight centrifugal tendency (Fig. 7). But arrangement is by no means rosette like. It may be near to Type II by Wagner-Weyrauch (cf. p. 132). However, it is dubious whether this type can always be distinguished from Type I. Anyhow, as noted in **SA-2**, the arrangement in Fig. 7 should have resulted by continuous dislocation of older cocoons as suggested by numerous post-emergence batches fallen sideways and 21 post-emergence batches lying on the nest bottom.

Miscellaneous notes: 1) Size of some batches, especially of Group 2, was very

Table 6. Batch composition in *B. diversus tersatus* Nest **DT-1.** Diameter not measured for all cocoons. Batch group 1 all *Ct.* Level=from nest bottom (cf. Fig. 7).

Batch			Cocoon diameter (mm)							Contents
No.	Level	Size	5	6	7	8	9	10	12	
1-1	1	20		3	10	6	1			
2	〃	18	2	1	7	5	3			
3	〃	12				12				
4	〃	7			1	6				
5	〃	12		2	7	3				
6	〃	16		1	3	10	2			
7	2	13		2		3				
8	1	12				8				
9	2	17		3	2	3	3			
10	1	6								
11	〃	15		3	6	2				
12	〃	18		2	2	14				
13	2	11		2	2	7				
14	3	16			2	14				
15	2	12			3	9				
16	〃	7				1	6			
2-1	〃	11		4	7					10 *Ct.i*, 1 *Hh*
2	〃	17			3	6	8			5 *Ct*, 10 *Hhx*, 2 *Hcx*
3	3	7						7		2 *Ct*, 1 *Cy*, 1 *Hhx*, 1 *Hhy*, 2 *Ld*
4	2	10			8	2				1 *Ct*, 5 *Ci*, 4 *Hhx*
5	3	15	1		6	6	2			9 *Ci*, 1 *Cy*, 2 *Hhx*, 3 *Hcx*
6	〃	12		5	1	2	4			10 *Ct*, 2 *Hhx*
7	1	20		6	4	10				2 *Ci*, 7 *Cx*, 6 *Hhx*, 5 *Hcx*
8	〃	14		2	12					8 *Ci*, 6 *Hhx*
9	〃	6		2	1	3				4 *Ci*, 1 *Cx*, 1 *Hh*
10	〃	16	1		1	14				14 *Ci*, 2 *Hhx*
11	1?	11		1	4	6				2 *Ci*, 8 *Hh*, 1 *Awd*
12	1	18		3	5	10				16 *Ct.i*, 2 *Hh*
13	3	17		1	1	6				11 *Ci*, 4 *Hh*, 2 *Hcx*
14	1?	20		3	4	6				18 *Ci*, 2 *Hcx*
15	2	11				4	3			2 *Ci*, 5 *Cx*, 4 *Hcx*
16	3	12		2	2	8				10 *Ci*, 2 *Hh*
17	1	14				4	10			5 *Hh*, 4 *Hhx*, 5 *Hcx*
18	3	14							14	1 *Ci*, 7 *Cx*, 3 *Hhx*, 3 *Hcx*
19	2?	24		1	3	15	5			20 *Ci*, 1 *Hhx*, 3 *Hcx*
20	4	14					9			6 *Ci*, 1 *Hhx*, 5 *Hcx*, 1 *Ld*
21	2	24				16	8			7 *Ci*, 17 *Hcx*
22	〃	24					24			7 *Ci*, 4 *Cx*, 3 *Hhx*, 10 *Hcx*
23	1	9					9			5 *Ci*, 1 *Cy*, 3 *Hhx*
24	〃	12				8				4 *Ci*, 3 *Cx*, 1 *Hhx*, 4 *Hcx*
25	〃	15	1	1	1	12				10 *Ci*, 2 *Cx*, 2 *Hhx*, 1 *Hcx*
26	2	17		2	3	6	5	1		4 *Cx*, 9 *Hh*, 4 *Hcx*
27	〃	10				2	8			2 *Cx*, 6 *Hhx*, 2 *Hcx*
28	〃	22				3	19			11 *Cx*, 6 *Hhx*, 5 *Hcx*
29	3?	5			2	3				3 *Ci*, 1 *Hhx*, 1 *Hhy*
3-1	3	5						4		5 *Am*
2	〃	9					3	6		3 *Ci*, 5 *Am*, 1 *Pym*
3	2	5						4		2 *Ci*, 1 *Am*, 2 *Pom*
4	〃	5						4		3 *Ci*, 2 *Am*
4-1	3	5						5		5 *Pom*
2	〃	7					2	5		7 *Pom*
3	2	10					3	6		10 *Pom*
4	3	7						7		7 *Pom*
5	?	10					2	8		10 *Pom*
6	3	6						6		6 *Pom*

large, possibly being composite batches. 2) Egg cells were mostly built on tops of cocoons with young pupae or prepupae, rarely at niches of cocoons, relatively tall and not primed with pollen. 3) Katayama (1965) recorded egg cells of *B.d. diversus* as usually built one per cocoon, if two, separated from each other. In **DT-1** most cells were built in contiguity (Fig. 7 and composition given above), some ones even

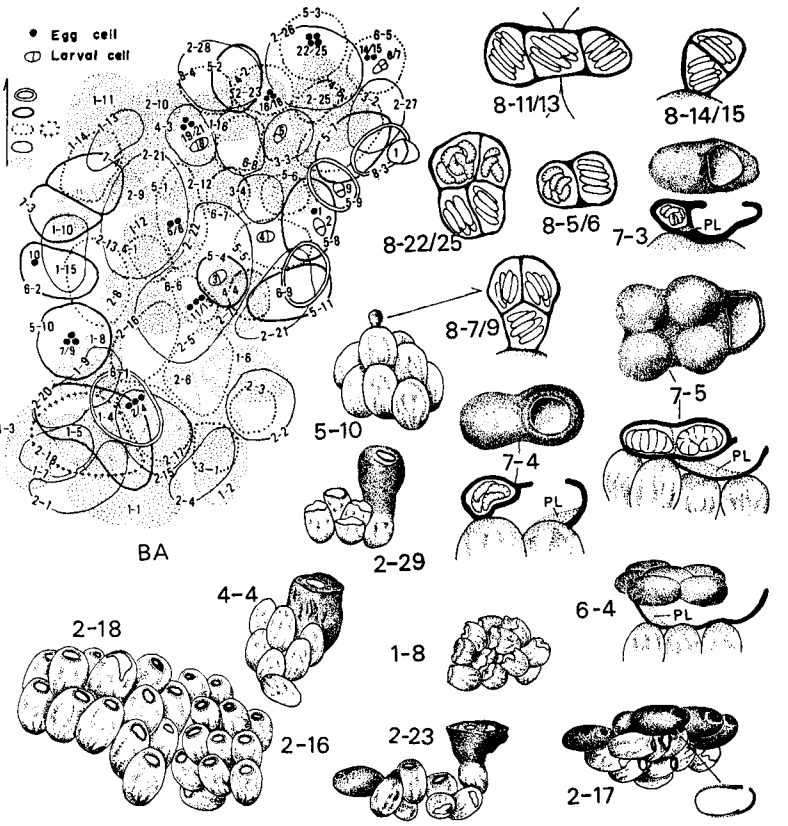

Fig. 7. *B. diversus tersatus* Nest **DT-1**. Top left. Batch arrangement (Queen batch 2–18 shown with cross contour, egg and larval cells given without group number, e.g. 22/25 instead of 8–22～8–25). Some particular batches shown with Arabic No. Egg cells (8-*n*). 5/6, 11/13, 22/25 (two cells or more built in contact), 14/15, 7/9 (ditto, one cell or two above another); Larval cells with pockets (7–3, 4, 5). In all cells pockets are separated from cell interior by wax partition (dotted=pollen). 3=with just emerged larvae, a small pollen mass on cell bottom; 4=bottom of pocket not lined with wax; Batches with cocoons. 6–4=with spinning larvae and remain of pocket, 2–23, 29=one cocoon transformed in storage pot receiving wax overgrowth, 2–18/2–16=queen and worker batches, 4–4=with a large wax pot, 1–8=all torn and fallen sideways, 2–17=ditto, but some cocoons wax-coated and filled with honey.

above others. Possibly these were worker built, though eggs were mostly laid horizontally, never irregularly as in some species (cf. p. 129 and **HS-1**). 4) All feeding pockets were updirected. Curiously the pocket and cell interior were separated by wax wall in B 7-3, 4 and 5 (Fig. 7), nevertheless, 7-3 contained a small pollen mass on the bottom and pockets of 7-4, 5 and of a post-feeding batch 6-4 were provided with pollen. Thus, the pockets in these cells were functionally equivalent to pollen pots. In 7-4 the bottom of the pocket was not wax-lined. 5) Numerous cocoons, even some ones fallen sideways (Fig. 7, 2-17) were used for honey storage. Five cocoons were provided with wax overgrowth upon the orifice (Fig. 7, 2-23, 2-29). There were 3 empty pots, one being very large (1.8 cm h and 1.3 cm w, Fig. 7, 4-4). 6) Gradual enlargement of cocoon diameter in later batches is traced but not so clear as in **DD-12** and *Thoracobombus*. Size variation in females, age- and size-linked worker polyergism and ovarian development in workers are referred to pp. 138~144 and (Fig. 15~18, Tables 14, 15, 17).

DT-2 (Fig. 8). Zenibako near Sapporo, September 27, 1965, taken by Mr. T. Matsumura and S.F.S. In an underground cavity in the floor of a shaded larch forest (Fig. 6, DT-2). Entrance hole 3.5 cm wide, nest canal first horizontal, then descending steeply (lost at middle). Nest cavity 39 cm deep, 10×15 cm large, and

Table 7. Batch composition in *B. diversus tersatus* Nest **DT-2**
(Batches 1-*n* mostly *Ct*)

Batch			Cocoon diameter (mm)						Contents
No.	Level	Size	5	6	7	8	9	12	
1-1	1	8			8				
2	〃	7			4	3			
3	〃	9		1	5	3			
4	〃	12		1	7	4			
5	〃	11		2	9				
6	2	16		2	14				
7	〃	7		2	4	1			
8	〃	7			3	4			
9	1	5		1	4				
10	2	8	1	2	4	1			
11	〃	11							
2-1	3	12		2	5	5			2 *Ci*, 10 *Hhx*
2	2	12		8	4				10 *Ci*, 1 *Cx*, 1 *Hhx*
3	〃	14			10	4			11 *Ci*, 3 *Hhx*
4	4	18		3	14	1			5 *Ct*, 7 *Ci*, 6 *Hhx*
5	3	12		2	5	3	2		4 *Ci*, 8 *Hhx*
6	〃	17		2	9	6			14 *Ci*, 3 *Hhx*
7	〃	6						6	5 *Hh*, 1 *Hhx*
8	4	10						10	10 *Hh*
3-1	2	8		5	2	1			2 *Ci*, 4 *Hh*, 1 *Hcx*, 1 *Pow*
2	5	13			2	1		10	1 *Ciq*, 5 *Aq*, 3 *Poq*, 1 *Pyq*, 1 *Prd*, 1 *Prd*, 2 *Ld*
3	〃	16						16	16 *Prq*

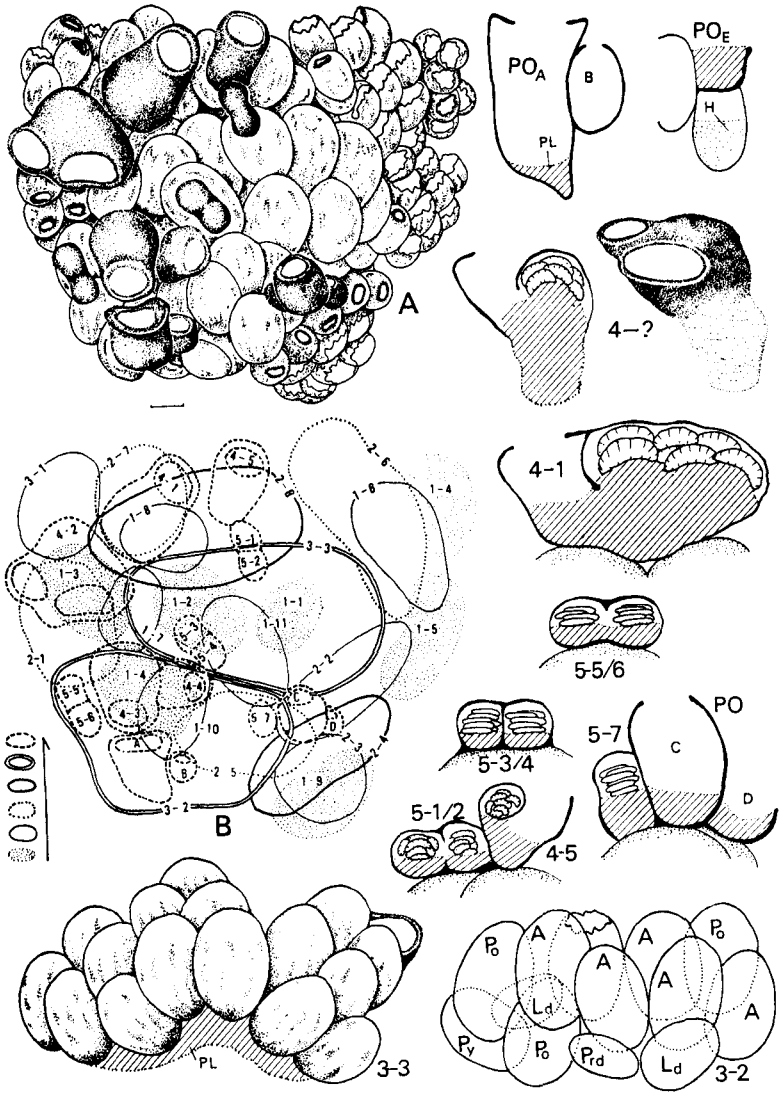

Fig. 8. *B. diversus tersatus* Nest **DT-2.** A. Horizontal view. B. Ditto, batch arrangement (scale=1 cm, storage pots shown alphabetically). PO$_i$ (i=A~E)=wax pollen pots; 4–1,2,5=larval cells with feeding pockets, 4–2 with two pockets and pollen mass exposed below; 5–1~7=egg cells, all primed with pollen; 3–3=queen batch, with vestige of pocket at right and thick amorphous pollen deposit below; 3–2=mixed batch. A (adult), Po and Py (old and young pupae)=queens, L (larva) and Pr (prepupa) (all dead=d)=males or workers.

about 50 cm distant from entrance. Nest mass 7 cm in diameter, outer cover 3 cm thick, wax envelope absent. Virtually no attack at nest removal.

Population: Adults Foundress + 13 new *Q*+51 *W*, ca. 5 *W* escaped. Cocoons 210 *C* (52 *Hh*)+5 *Aq*+4 *Pq*+16 *Prq*+1 *Pow*+1 *Prd*+2 *Ld*=239. Pre-cocoons 54 *L* (7 cells) and 45 *E* (5 cells). Batches were classified in 5 groups: 1. Post-emergence cocoons, mostly *Ct*. 2. Ditto, mostly *Ci*. 3. Some cocoons with immatures. 4. Larval cells. 5. Egg cells. Batch composition of groups 1~3 in Table 7, and of groups 4~5 as follows: 4–1 (9 *Lo*), 2(7 *Lo*), 3(8 *Ly*), 4(7 *Ly*), 5 (9 *Ly*); 5–1/2 (7 *Ly*/7 *Ly*), 3/4 (8 *E*/10 *E*), 5/6 (10 *E*/7 *E*), 7 (10 *E*). Percentage ratio queen cocoons/total cocoons (42/239)=17.6%.

Colony conditions: Attained the climax in spite of a relatively small colony size. Egg cells built in contiguity suggest the appearance of laying workers, but eggs were laid regularly. Worker ovaries were not examined. Most new *QQ* formed pure batches except B 3–2 (Fig. 8).

Miscellaneous notes: Batch arrangement (Fig. 8, B) is basically similar to that in **DT-1**. This nest was particular in some points (Fig. 8). 1) Egg cell tall, built on tops of cocoons, all except B 5–7 in contiguity and eggs laid horizontally as in DT–1. 2) Wax partition separating egg cells very thin in B 5–3/4 (0.6 mm thick) and incomplete in B 5–1/2 and 5/6. 3) All egg cells primed with pollen, a trait so far not observed in *B. diversus*. Pollen mass very thick in B 5–7, resulting in a very tall cell. 4) Many larval cells provided with excessive pollen mass (cf. Fig. 8, 4–1, 4–5), and the feeding pockets normally communicated with the cell interior. In B 4–2 with 2 pockets, pollen mass very tall, nearly cylindrical and its basal half virtually without wax cover. Structure of B 4–5 also implies a conspicuous modification after hatching out of larvae. 5) Most honey containing cocoons with a thick wax lining at orifices. There were 5 pollen pots, A~E, each being particular. A was elongate and the small one, B, was built on the side wall of A. C and D were contiguous with B 5–7 (cf. the absence of communication between pocket and cell interior in **DT-1**), and E was built upon a cocoon half-filled with honey. 6) Base of B 3–3, a queen batch, was filled with a thick (6 mm) amorphous pollen mass not covered with wax. 7) Vestige of pocket by a queen batch 3–3 proves feeding of queen larvae through pockets. Size variation in females and age- and size-linked polyergism referred to pp. 136~142 (Fig. 15, 17~19, Tables 14, 15).

Bombus (Bombus) ignitus Smith (=Ig)

B. ignitus is the most southerly adapted species among Japanese bumblebees, being relatively common in lowlands of Central Japan, though less than *B. d. diversus*. Nest and behavior of "*B. ignitus*" were recorded by Katano (1948), Nakatake (1951), Hashimoto (1958), Miyamoto (1963a, b) and Katayama (1967, '71, '73). But the females of *B. ignitus* is isochromic with those of *B.* (*Pyrobombus*) *ardens ardens*. Katano indubitably observed *B. a. ardens* (judging from the notes given for males) and probably Hashimoto also did the same error (from note on early colony dissolution characteristic to *ardens* and nesting site strange to *ignitus*). A subterranean nest observed by Nakatake (Miyazaki Pref.) could be of *B. ignitus*, but the description is very poor. The first authentic record is those by Miyamoto

(Sasayama, Hyogo Pref.) though she used the name *B.* (*Pratobombus*=*Pyrobombus*) *ignitus*. Nest (**Ig-A**) in an underground cavity 30~40 cm deep. Excavated on September 6. Foundress + 8 new *Q*+ 31 *W* + 51 *M*. 161 *C*+24 *Pm* + 2 *Pr*.

Up to the present E.K. collected 9 nests, all in Yaita, Tochigi Pref., all built in underground cavities, mostly being old burrows of small mammals. Only **Ig-9** is fully described below.

Ig-1. Early September, 1954. In a slope facing a bamboo thicket (45 cm deep). No foundress + ca. 90 *W*+ca. 50 sexuals. Cocoons ca. 800 including ca. 250 *Q* ones. A climax nest having produced many sexuals. Ratio queen cocoons/total cocoons=ca. 31%.

Ig-2. Early May, 1955. In a bank of a creek (30 cm deep). Foundress + 6 *W*. Cocoons ca. 20. Early nest. Transferred in an observation box but the foundress escaped.

Ig-3. Mid June, 1956. In a deciduous broad leaved forest (20 cm deep). Foundress + ca. 25 *W*. Cocoons ca. 55. Early nest.

Ig-4. Late August, 1956. In a slope facing a deciduous broad leaved forest (60 cm deep). No foundress+80 new sexuals +ca. 130 *W*. Cocoons ca. 1,300 (ca. 400 *Q* ones). The largest bumblebee nest so far recorded in Japan. Ratio queen cocoons/total cocoons=ca. 31%.

Ig-5. Early July, 1958. In a deciduous broad leaved forest (30 cm deep). Foundress +ca. 40 *W*+2 *Wd* infested by conopid fly. Cocoons ca. 90. Middle stage nest before queen production.

Ig-6 (=Katayama 1967, Colony A). July 21, 1963. In a *Cryptomeria* forest (35 cm deep, canal 72 cm long). Outer cover thin, wax envelope partial. Foundress+ca. 60 *W*. Cocoons 364 (21~29 batches, *Cq*=52). Ratio queen cocoons/total cocoons=14.3%.

Ig-7 (=Katayama 1967, Colony B, 1971 Colony A). June 28, 1964. In a *Cryptomeria* forest (14 cm deep, canal 23 cm long). Outer cover poor, containing a mummified vole, wax envelope partial. Foundress +77*W*+2*Wd* infested by conopid. Cocoons 113 *C*+61 pre-emergence (all *WW*)=174. Pre-cocoons 6 larval cells+8 egg cells. The nest was transferred in an observation box and produced in total 245 cocoons till August 12 (no *Q* produced).

Ig-8 (=Katayama 1967, Colony C). July 12, 1964. In an oak forest (8 cm deep, canal 93 cm long). Outer cover thick, wax envelope absent. No foundress +45 *W*+1 *Wd* infested by conopid. Cocoons 149 *C* (13 batches)+ 21 pre-emergence (2 batches, all *WW*)=170. No queen produced. Most cocoons without food. Possibly the foundress died in earlier stage.

Ig-9 (Fig. 9,=Katayama 1971, Colony B). June 28, 1970. In a steep slope of a *Chamaecyparis* forest, 6~8 m high and completely shaded. Entrance hole 1.5× 2 cm, canal descending perpendicular to 25 cm, then running for 55 cm parallel to the slope (Fig. 6, Ig-9). Nest cavity, being an abandoned vole nest, ovoid, 21 cm deep, thickly filled with decayed leaves. Wax envelope well developed.

The nest was transferred into an observation box and observed until the

disappearance of all bees from the box on September 19.

Population: Foundress + 28 *W*, 67 cocoons +10 larval cells+4 egg cells at nest removal. Batch composition: B 1 (10 *Ci*), 2(9 *Ci*+*Hh*, 1 with *Mutila*), 3(11 *Ci*+*Hp*), 4~7 (*Ci*+immatures), 4(8), 5(9), 6(7), 7(7), 8(8 *Pr*), 9~17 *L*, 18~21 *E*.

Subsequent development in observation box (unless mentioned, all successfully produced adults): B 1~40=*W* batches. B 4(8), 5(9), 6(7), 7(7), 8(8), 9(4), 10(7), 11(6), 12(6), 13(8), 14(9), 15(6), 16(6), 17(5), 18(5), 19(4), 20(6), 21(6), 22(8), 23(6), 24(7), 25(4), 26(9), 27(15), 28(8), 29(7), 30(1), 31(7), 32(9), 33(8), 34(6), 35(6), 36(8), 37(15), 38(9), 39(8), 40(7); B 41~48=*W* or *M* batches. 41(4 *W*+5 *M*), 42 (8 *W*), 43 (4 *W*+4 *M*), 44(7*M*), 45 (8 *M*), 46 (2 *W*+5 *M*), 47(6 *Pmd*), 48 (1 *W*+5 *M*); B 49~57 all *M* batches. 49 (7), 50(6), 51(5), 52 (8, 7+1 *d*), 53(1 *Pd*), 54(6), 55(8), 56(9), 57(9); 58 (1 *W*+6 *M*), 59 (1 *W*+5 *M*); B 60~90 all *M* batches. 60(12), 61(6), 62(8), 63(15), 64(7), 65(8), 66(6), 67(4), 68(7), 69(8), 70(6), 71(2+3 *d*), 72(3), 73 (3+3 *d*), 74(6), 75(3+2 *d*), 76(3), 77(1), 78(1), 79(2+1 *d*), 80(2), 81(1), 82(2), 83(4), 84(3+1 *d*), 85(1+1 *d*), 86(1), 87(2), 88(2), 89(3+1 *d*), 90 (1+3 *d*).

Total cocoons 575 (258 or 44.9%=*MM*). B 83~90 were built and laid by workers, producing 23 *M*, i.e. 8.9% of total *MM* produced, though workers laid as many as 833 eggs (Katayama 1971), many of which were artificially removed or abandoned by workers.

Colony conditions: After transference in the observation box, the foundress survived to August 14 and actively laid for a considerable time (to B 82 on August 12) but produced no *Q*.

Miscellaneous notes: As the nest was taken at an early stage, batch arrangement was clearly recognized, never exhibiting Type I by Wagner-Weyrauch (Fig. 9, Ig–9). Beside honey stored in cocoons, there were 2 large honey pots. One cocoon of B 2 contained a dead male of *Mutila europaea mikado*. In the lowlands of Central Japan *B. d. diversus* and *B. a. ardens* are often infested by *Mutila* but so far no infested nest of *B. ignitus* has been reported. This species effectively removes the

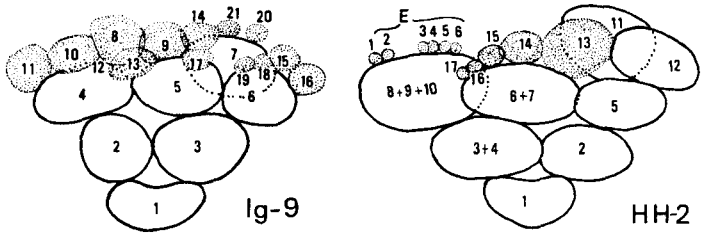

Fig. 9. Batch arrangement (lateral view) of *B. ignitus* Nest **Ig-9** and *B. hypocrita hypocrita* Nest **HH-2**. Solid contour=cocooned batches, dotted=larval cells, E=egg cells.

invaded *Mutila* (Miyamoto 1963 b, Katayama unpubl.). The present case is the first record of infestation. Some notes on nest structure: 1) Egg cells built on post-spinning, never on spinning cocoons, either isolately or in group. They were relatively tall and mostly built on the tops of cocoons. 2) Batches involving spinning larvae very loosely attached one another and walls of such cocoons very thin,

early torn as those in *B. h. hypocrita* and *B. h. sapporoensis* (cf. HS–1, p. 149).

Bombus (*Bombus*) *hypocrita hypocrita* Pérez (=HH)

This form is distributed in higher altitudes than *B. ignitus* (cf. p. 127) in Central Japan. Two underground nests were discovered in Shiobara (700~750 m), Tochigi Pref. by E.K. and oviposition habits and colony development were observed (Katayama 1974, '75). Here some findings at nest removal are recorded (**HH-1**, **2**=Colony A, B in Katayama 1974).

HH-1. August 29, 1971. In a steep SSW facing slope of a low mixed forest of oak and *Cryptomeria* (2.5 m tall). Ground surface covered with a 3~5 cm thick layer of fallen leaves. Entrance hole 3.8×2 cm, nest cavity 22 cm deep, with linear distance from entrance 31 cm, errect ovoid, 11×13×14(h) cm (Fig. 6, HH–1). Outer cover poor, consisting of dry leaves mixed with some torn pieces of old cocoons.[1] Wax envelope complete, connected with nest mass by many wax pillars.

Population: Foundress +40 *W* (mostly small or dwarf) + 13 *M*. Cocoons 298 *C*+5 *A*+ 30 *P*+ 7 *Pr*=340 (33 batches). Pre-cocoons 1 larval cell +1 egg cell.

Batch composition: B 1~24 all *Ci.t*, probably all *WW* (B 1~3 mostly *Ct*, heavily infested by mold; 4~11 many *Ct* and slightly infested by mold; 12~16 some cocoons *Hh*; 17~24 ditto, but much honey). B 1(7), 2(11), 3(14), 4(6), 5(6), 6(7), 7(6), 8(11), 9(8), 10(12), 11(11), 12(13), 13(13), 14(9), 15(9), 16(12), 17(6), 18(9), 19(6), 20(8), 21(12), 22(31), 23(14), 24(14); B 25~32 all *MM*, 25 (13), 26(10), 27(11), 28(10: 1 *A*+9 *C*), 29 (11: 4 *A*+7 *P*), 30(8 *P*), 31(10 *P*), 32 (4 *P*); B 33~35 probably all *MM*, 33 (4 *Pr*), 34 (*Ly*, not counted), 35(26 *E*). Further 4 detached cocoons (1 *Pm* and 3 *Pr*).

Colony conditions: The foundress survived till September 7, but no new *QQ* were produced. Total *MM* produced were 78 or 22.9%, probably many ones by laying workers. The egg cell (B 35) was certainly built and laid by laying worker or workers, judging from its anomalous position (built on a pollen pot), high egg number and irregular egg orientation.

Miscellaneous notes: There were 5 honey pots and 7 pollen pots with abundant pollen deposit. No cocoon with pollen. Honey stored in cocoons dense, but that in wax pots thin.

HH-2 (Fig. 9). July 9, 1972. In a mild W-facing slope of a *Cryptomeria* reforestation (0.8~1.5 m) mixed with oak and chestnut, with undergrowth of bamboo, *Miscanthes*, sedge, etc. Ground surface covered with fallen leaves 2~3 cm thick. Entrance hole triangular. Canal first mildly, then steeply and again mildly descending to nest cavity of 10×12×8 (h) cm in size, 37 cm deep and with linear distance from entrance 44 cm (Fig. 6, **HH-2**). Outer cover consisting of fallen leaves, dead grasses and mosses, admixed with some pieces of torn cocoons. Wax envelope present but partial. The nest was transferred into an

1) In such case, cocoons are never entirely broken. Hence, admixture of cocoon pieces does not make the count of old cocoons difficult (cf. also **HH-2**).

observation box and observed till September 20.

Population: At nest removal foundress + 31 *W*. Cocoons 66 *C* (B 1~7) + 23 *P* (B 8~10)+17 *Pr* (B 11~12)=106 (12 batches). Pre-cocoons 24 *L* (B 13~17), 28+ x *E* (B 18~23, cf. E 1~6 in Fig. 9, **HH-2**).

Batch composition after rearing (Total immatures/emerged adults, equal if unmentioned): B 1~44 all *WW*. 1(7/6), 2(12), 3+4(21), 5(7), 6+7 (19), 8+9+10(23/21), 11(10), 12 (7/6), 13(6), 14(6), 15(4), 16(6), 17(2), 18(7), 19(3), 20(6), 21(7), 22(5), 23 (destroyed at egg stage), 24(7), 25(6), 26(7), 27(6), 28(6), 29(6), 30(7), 31(6), 32(7), 33(6), 34~36(19/18), 37(6), 38(6), 39(6), 40(3), 41~42 (destroyed after hatching), 43(1), 44(6): B 45(7=6 *W*+1 *Q*), 46 (7=1 *W*+6 *Q*), 47(6=2 *W*+4 *Q*), 48(6M), 49(6=5 *Q*+1 *M*), 50(3 *M*), 51 (6=2 *W*+4 *Q*), 52(2=1 *W*+1 *Q*), 53(6=4 *W*+2 *Q*); B 54~65 all *MM*. 54(3), 55+56(6), 57 (dropped below B 55~56, impossible to grow), 58~60(9), 61(1), 62(3), 63(4), 64(6), 65(4). Two additional batches by laying workers, B W-1(9/8), 2(3/2).

Colony conditions: Discovered at an early stage and successfully developed under artificial conditions. Percentage ratio queen/total production is given in four ways. Total queen cocoons 23(Q), total cocoons produced 366 (T_1), total cocoons issuing adults 359 (T_2), total cocoons produced by foundress 354 (T_3), ditto, those issuing adults 349(T_4). $P_1=Q/T_1=6.3\%$, $P_2=Q/T_2=6.4\%$, $P_3=Q/T_3=6.5\%$, $P_4=Q/T_4=6.6\%$.

Miscellaneous notes: Batch arrangement at nest removal was similar to that in **Ig-9** (Fig. 9). Some cocoons contained honey and pollen. Besides there were 3 large honey pots. Both **HH-1** and **2** were not infested by *Mutila*. Admixture of torn pieces of old cocoons may relate with space economy. New *QQ* emerged on August 26~September 3 and *MM* on August 23~September 20. Departures of new *QQ* started on August 30. They returned to the nest without bringing food and stayed for 2~3 days before final departure. Within the nest they participated in no colony maintenance tasks including "brooding". Male departures started on August 27. Once departed, no *M* returned to the nest. During August 30~ September 7 many new *QQ* and *MM* stayed in the nest but no intranidal mating took place. These findings coincide with observations with *B. ignitus* (Katayama 1967) but not to those with *B. a. ardens* (Katayama 1964 and unpubl. data).

Observations on **HH-2** in the rearing box were published elsewhere (Katayama 1974, '75). Some of them and those on **HH-1** relating with nest structures are summarized. 1) Queen built egg cells relatively tall, built on cocoons with post-spinning larvae or pupae, never on those with spinning larvae. 2) Queen built cells tending to be made in contiguity. 3) Additional ovipositions by the foundress in an egg cell are rare, only seen after the appearance of laying workers (Katayama 1974, p. 427, p. 432). 4) Worker built and laid cells are variable in size and batch size, due to removal and addition of eggs by other workers. 5) Worker egg cells are also built in contiguity, but isolated cells are more frequent. 6) Queen eggs are laid horizontally and regularly. Worker eggs and those by foundress after the appearance of laying workers are laid irregularly. 7) Translocation of batches (and each cocoon) is very frequent. 8) Spinning queen larvae are fed through

permanent apertures for 4～5 days, but worker and male larvae for 2～3 days.

Bombus (*Bombus*) *hypocrita sapporoensis* Cockerell (=HS)

This form is common in Hokkaido horizontally as well as altitudinally. S.F.S. found traffic of workers at holes on the ground three times but only one nest was excavated.

HS-1 (Fig. 10, 11). Campus of Hokkaido University, July 15, 1959. In an underground cavity in an open area covered with grasses about 30 cm tall. During July 9～15 all homing workers landed at a spot 30 cm apart from the entrance hole and went to the hole on foot (Fig. 6, **HS-1**, L-e). This platform was sparsely covered with cut pieces of dead grasses. Often some workers ran on the platform keeping such pieces in mouth. Entrance hole ca. 7 cm wide, but narrowed to 3 cm with pieces of dead grasses. Canal 7～10 cm wide, first gently descending, then running nearly horizontally till nest cavity, possibly an abandoned rat's nest, lying 20 cm deep and 80 cm distant from entrance, 20×25×16(h) cm. Floor of

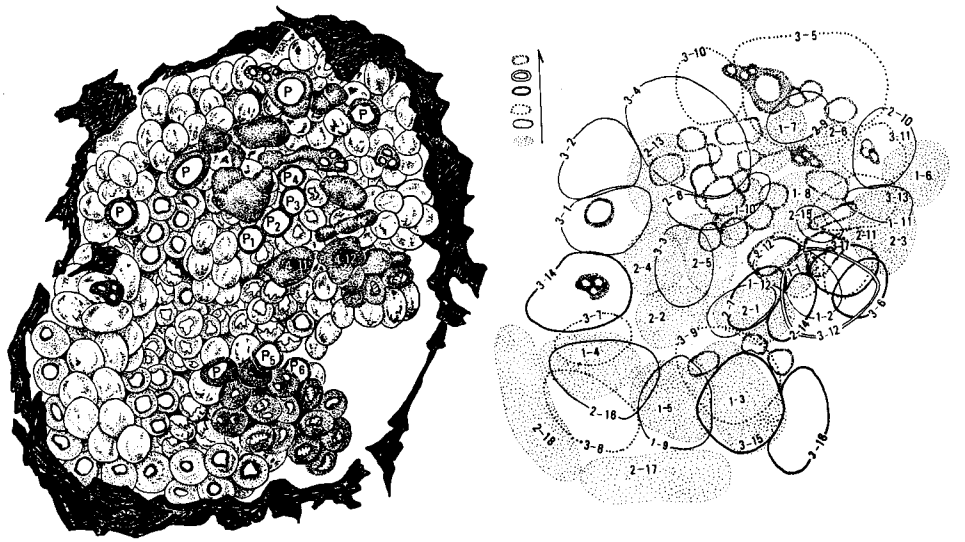

Fig. 10. *B. hypocrita sapporoensis* Nest **HS-1**. Left. Horizontal view (wax envelope removed, P=pots, some ones numbered). Right. Batch arrangement. Batch No. of two larval cells given in left figure, and of others and all egg cells in Fig. 11, B.

both canal and nest cavity sparsely covered with cut pieces of grasses. Outer nest cover about 1 cm thick, consisting of cut pieces of grasses. Wax envelope dark brown and complete. At nest removal many workers took upside down defensive posture and some ones ejected feces to a distance of 3 cm, but positive attack was weak.

Table 8. Batch composition in *B. hypocrita sapporoensis* Nest **HS-1**

Batch			Cocoon diameter (mm)										Contents
No.	Level	Size	5	6	7	8	9	10	11	12	14	15	
1-1	1	11	1	2	6	2							11 *Ct*
2	2	14			1	7	4	2					14 *Ct*
3	1	9				2	7						9 *Ct*
4	〃	7					3	2	2				7 *Ct*
5	〃	10					2	8					10 *Ct*
6	〃	7				6	1						7 *Ct*
7	〃	7					7						7 *Ct*
8	〃	8				3	4	1					7 *Ct*, 1 *Hh*
9	2	8						4	4				6 *Ct*, 2 *Hh*
10	1	8		1	6	1							1 *Ct*, 3 *Cix*, 1 *Hh*, 3 *Ld*
11	2	6						6					6 *Ct*
12	〃	8						8					8 *Ct*
2-1	1	13			1	12							1 *Ct*, 6 *Ci*, 3 *Hh*, 3 *Hhx*
2	〃	7					7						2 *Ct*, 2 *Ci*, 3 *Hhx*
3	〃	21				2	19						10 *Ct*, 7 *Ci*, 3 *Hh*, 1 *Hhx*
4	〃	10					10						7 *Ci*, 3 *Hhx*
5	〃	8				2	5	1					1 *Ci*, 7 *Hhx*
6	〃	8					8						3 *Ci*, 1 *Hh*, 4 *Hhx*
7	3	11			1	6	1						2 *Ci*, 1 *Cx*, 2 *Hh*, 6 *Hhx*
8	2	10				10							2 *Ct*, 4 *Ci*, 4 *Hhx*
9	〃	9					9						2 *Ct*, 2 *Ci*, 2 *Hh*, 3 *Hhx*
10	〃	10				1	9						1 *Ct*, 7 *Ci*, 2 *Hh*
11	1	7						7					1 *Ct*, 3 *Hh*, 3 *Hhx*
12	3	8						8					1 *Ct*, 2 *Hh*, 5 *Hhx*
13	1	14					11	3					2 *Ct*, 3 *Ci*, 5 *Hh*, 4 *Hhx*
14	4	11						11					1 *Ct*, 5 *Ci*, 1 *Hh*, 4 *Hhx*
15	2	5						5					2 *Ci*, 2 *Cx*, 1 *Hh*
16	〃	7								7			7 *Hhx*
17	1	6									3	3	3 *Ci*, 3 *Hhx*
18	〃	7									3	4	4 *Ci*, 3 *Hhx*
3-1	2	10						10					1 *Am*, 7 *Pom*, 2 *Pym*
2	〃	8						6	2				2 *Ci*, 4 *Am*, 1 *Pom*, 1 *Pym*
3	〃	5							5				2 *Ci*, 2 *Pom*, 1 *Pym*
4	〃	28							28				10 *Am*, 17 *Pom*, 1 *Pym*
5	3	26							26				3 *Pom*, 22 *Pym*, 1 *Pyw*
6	4	4									2	2	2 *Ci*, 2 *Aq*
7	3	4									3	1	4 *Poq*
8	〃	6									1	5	4 *Aq*, 2 *Pop*
9	〃	9									4	5	5 *Ci*, 2 *Aq*, 2 *Poq*
10	〃	7							7				7 *Pym*
11	〃	4						4					4 *Pym*
12	5	10						10					4 *Pym*, 6 *Pr*
13	2	6						6					1 *Pym*, 5 *Pr*
14	4	8						8					5 *Ci*, 3 *Pom*
15	〃	6											6 *Pr*
16	〃	10											2 *Pym*, 8 *Pr*
17	6	7											7 *Pr*

Population: Adults No foundress +96 *W*+12 new *Q*+33 *M*. Cocoons 291 *C* (92 *Hh*+3 *Ld*)+23 *A* (8 *Q*+15 *M*)+87 *P* (8 *Q*+1 *W*+78 *M*)+32 *Pr*=433. Pre-cocoons 28 *L* (2 *d*)+75 *E*. Batches were classified in 5 groups: 1. Post-emergence, mostly *Ct*, only partly *Hh*. 2. Ditto, mostly *Ci*, many *Hh*. 3. Cocoons with *A*~*Pr*. 4. Larval cells. 5. Egg cells. Batch composition in groups 1~3 in Table 8, and that in groups 4 and 5 as follows: 4–1(3), 2(1), 3(4 *d*), 4(1), 5(7), 6(1), 7(1), 8(1), 9(2), 10(6), 11(2), 12(3), 13~15 (1, some lost during nest removal); 5–1(5), 2(27), 3(43), 4~12 (empty, B 4 and 2 with honey, 5 with honey on some dead eggs).

Colony conditions: In spite of a relatively early date, the colony already produced new *QQ*. The foundress died after producing 36 new *QQ* (20 emerged, all from pure queen batches) and at least some males (cf. B 3–5=mixed batch, Fig. 11, E). Nest contained many laying workers, which must have produced

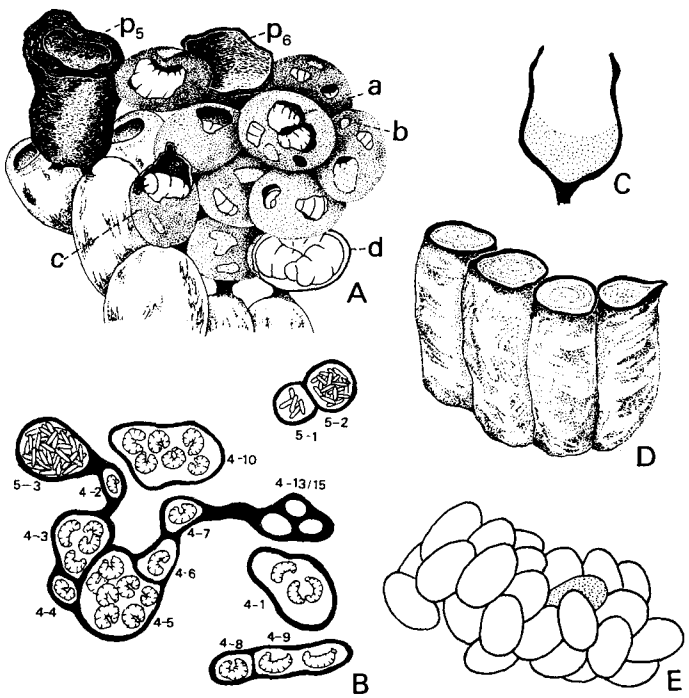

Fig. 11. *B. hypocrita sapporoensis* Nest **HS-1** (Continued). A. Batch 3–15 (cf. Fig. 10) with spinning larvae. a=cocoon wall broken, exposing larva, b=broken window partly covered with thin film, c=cocoon dropped down, supported only by a part of torn wall, d=spinning larva shown by removing cocoon wall, P_5~P_6=storage pots; B. Egg and larval cells at center, showing contents (5–1~3=egg cells, others with larvae); C. Pollen pot (P_6, cf. Fig. 10 and Fig. 11 A) with pollen. D. Pollen pots P_1~P_4 (cf. Fig. 10 left), cylindrical, built in contiguity and wax cover being incomplete except top; E. Mixed batch. All with dark eyed male pupae except one pink eyed worker pupa (dotted).

numerous males.

Miscellaneous notes: 1) Batch arrangement (Fig. 10) was quite irregular, similar to that of **DT-1** (Fig. 7). Stratification was most conspicuous at the right side middle. 2) At nest removal it was noticed that batches including spinning larvae (Fig. 10, B 3–15, 16, 17) were very loosely attached one another, easily detaching from the mass (Fig. 11, A-c). Walls of such cocoons are very thin, easily torn, exposing larvae (Fig. 11, A-a), who closed such apertures with flimsy silk (Fig. 11, A-b). 3) Many egg and larval cells were built in contiguity, forming a string (Fig. 10, and 11 B). Many egg cells were empty or filled with honey. Eggs in 3 cells were arranged very irregularly, and 2 cells contained very many eggs (Fig. 11, B, 5–1/3). All these anomalies should have been related with laying workers (cf. Katayama 1971, '74). 4) There were 12 pollen pots (P in Fig. 10 and Fig. 11, C, D). Among them $P_1 \sim P_4$ were built contiguously at the nest center and very tall, $11 \sim 12$ mm in diameter and 28 mm high as recorded in some consubgeneric species (cf. Sakagami 1976, pp. 411, 435), but covered with wax only at the uppermost part (Fig. 11, D). Size variation in females and ovarian development in workers are referred to pp. 132~135 (Fig. 15, Tables 14, 17).

Bombus (*Pyrobombus*) *beaticola beaticola* (Tkalců) (=BB)

A single, very incipient nest of this alpine form was collected by Mr. M. Munakata and sent to S.F.S.

BB-1 (Fig. 12). Futamata, Ô-Kambazawa (2,300 m), Akaishi Mts., Nagano Pref. July 18, 1976. Alpine meadow above timber line. In a small cavity under a large rock 3 cm below ground surface. Nest built in a small space among dense root systems of *Cassiope*. Nest mass covered with a disk (2 cm in diameter) of dry leaves consolidated with wax.

Population: No foundress +3 *W*. One cocoon batch (5×6 cm) alone, with 8 cocoons. Central 4 post-emergence, peripheral ones with *Awd*. Four egg cells

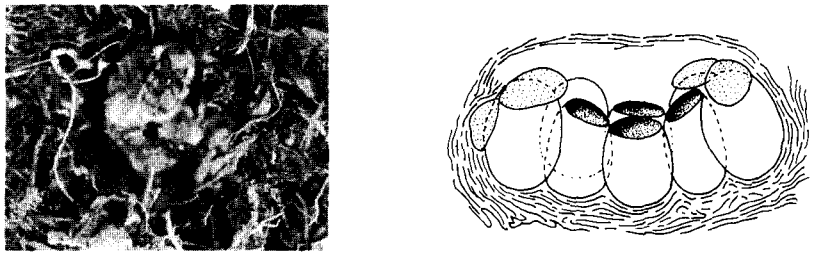

Fig. 12. *B. beaticola beaticola* Nest **BB-1.** Left. Nest cavity. Right. Batch arrangement and plant cover. Dotted=egg cells.

built on peripheral cocoons, each containing 3, 2, 3 and x small dead larvae. It is uncertain whether the foundress died after building 4 egg cells or these were built and laid by orphan workers.

Bombus (*Pyrobombus*) *ardens ardens* Smith (=AA)

This form is common in hilly areas and low mountains of Honshu, Shikoku and Kyushu, and characterized by a brief colony cycle. Sexuals appear in June and all colonies die in July (Miyamoto 1957 b). The females are isochromic with *B. ignitus*, so that care must be taken in studying nests. First, reliable previous records are summarized.

Katano (1948, published as *B. ignitus* but indubitably *B. a. ardens*, cf. *B. ignitus*). **AA-A.** Usune-Mura, Gumma Pref., June 26. In an underground cavity of a bamboo stand, 20~30 cm long. 40 *Q*+ more than 120 *W*+ some *M*.

Miyamoto (1957 a). **AA-B.** Sasayama, Hyogo Pref., late May. Underground nest in a bank. Collapsed after producing 14 *W*.

Miyamoto (1957 b). **AA-C.** Sasayama. Discovered on May 31. The first *M* flew on June 3. Nest removed on July 13. In a shallow underground cavity in a bamboo thicket. Ground surface covered with bamboo leaves 10~15 cm thick. Cavity 5~8 cm below ground surface, i.e. 15~20 cm below the surface of fallen leaves. Entrance canal 1 m long. No attack at nest removal. Wax envelope present. Foundress+17 foragers +3 house bees. Except one large house bee all *WW* with undeveloped ovaries. 50 *C*+ 29 *Pm* and 2 honey pots.

Katayama (1964, cf. below, **AA-7, 8**).

Tsuneki (1970). **AA-D.** Nikko, Tochigi Pref., June 12. In a shallow underground cavity (seemingly without wax envelope). Foundress +2 new *W*. 12 batches: 1 (2*A*, some *C* scattering on the cavity bottom possibly belonging to this batch), 2(7 *Po*), 3(6 *Py*), 4~11 (all *LL*, each 9, 6, 5, 18, 9, 6, 2), 12(3 *E*) and 3 honey pots. A very incipient nest. Number of *WW* abnormally small compared to that of immatures. Judging from the accompanied figure, nest mass seems very compact. **AA-E.** Arashi-Mura, 800 m, Fukui Pref., June 27. In a pile of straws placed on the shelf of a hut, 2 m above the ground. Foundress +12 homing *W*+7 young *W*; 25 *C*+15 *P* or *Pr*, and 7 larval batches built in contiguity (each with 6, 6, 6, 6, 5, 4, 4 *L*).

Up to the present, one of us (E. K.) has discovered 11 nests in Tochigi Pref., **AA-10**, **11** in Shiobara, all others in Yaita. Only **AA-11** will be described in detail. B. *a. ardens* is polymorphic in northern to central Honshu (Sakagami and Ishikawa 1969). Most females are dark brown with reddish tail as in *B. ignitus* but some ones yellow banded, the frequency of which increases northwards. In nests removed by E.K. adult females of the same nest were concolorous, both foundress and her offspring, e.g. **AA-1, 2, 7, 9, 10** were dark type and **AA-6, 8, 11** yellow banded, suggesting genetic control of hair coloration. Obviously, this is not expected at nest usurpation between queens of different coloration.

AA-1. Early May, 1952. In a pile of fallen leaves on the ground of a bamboo stand. Foundress +4*W*, about 20 cocoons (2 batches), 1 larval cell, several egg cells and 2 honey pots. An incipient nest. After transfer in an observation box another queen invaded. One was killed but as both nest owner and invader queens were non-yellow banded, it is unknown whether she was either. Only some *MM* were produced in mid June.

AA-2. Early May, 1953. In a space between earthen wall and a large rock, 90 cm above the ground. Imposible to take.

AA-3. Late April, 1954. In a shallow undeground cavity in an oak-chestnut

forest. Foundress alone. First batch (ca. 10 cocoons), carrying several egg cells linearly connected upon the ridges along the median groove. An incipient nest.

AA-4. Mid May, 1954. In a shallow cavity near the base of a stump in an oak-chestnut forest. No foundress + ca. 15 *W* + a *B. diversus* queen. Cocoons ca. 40. Both *WW* and *diversus* queen excited and *WW* sometimes grasped the legs of the latter. Transferred in a box but the *diversus* queen was killed in the evening. A case of unsuccessful interspecific invasion between two remote species. The corpse of foundress was carelessly not confirmed.

AA-5. Early June, 1954. In an underground cavity (20 cm deep) in a *Cryptomeria* reforestation. Foundress + ca. 15 *W*. Cocoons ca. 70. No production of sexuals. Many cocoons with emergence hole of *Mutila europaea mikado* and many *Mutila* adults (both sexes) in the nest.

AA-6. Early June, 1955. In an underground cavity (35 cm deep) below a stump in a *Cryptomeria* forest. Foundress + ca. 70 *W*. Cocoons ca. 250 including many queen ones.

AA-7 (=Katyama 1964, Colony A). June 15, 1963. In fallen leaves piled on an abandoned field. Canal to entrance 27 cm. Nest mass 13.5×11×8.5 (h) cm. No foundress + 30 *W*+ca. 10 sexuals (new *Q*+*M*). Transferred in an observation box and reared until July 15. Total cocoons produced 634, of which 171 (27%) were queen ones, and 124 queens (72.5%) emerged.

AA-8 (=Katayama 1964, Colony B). June 16, 1963. In an underground cavity, probably abandoned by vole, in an oak-chestnut forest 2 m tall. No foundress + ca. 85 *W*+6 new *Q*+ many *M*+1 *Wd*. Transferred in an observation box and reared till July 20. Total cocoons produced 717 (269 *Q* or 37.5%, emerged *QQ* 181 or 67.3%).

AA-9 (=Katayama 1966 b, Colony A). May 10, 1964. In a very shallow abandoned vole nest (8 cm below ground surface) under a pile of fallen leaves (canal 23 cm long). Foundress + 7 *W* + 33 cocoons. Two dead *Q* and 5 *Mutila* ♀♀, all invaded from the outside. No queen production.

AA-10 (=Katayama 1966b, Colony B). May 29, 1966. In a sapce under a stone in a *Cryptomeria* reforestation. Foundress +9 *W*+45 cocoons+4 honey pots + 4 pollen pots. Seven *Mutila* ♀♀ invaded from the outside. No queen production.

AA-11 (Fig. 13). June 6, 1976. In a shallow underground cavity in a WNW facing slope of a pine-oak-chestnut forest. Entrance hole 2.5×1.5 cm. Canal horizontal, 2 cm wide and 16 cm long. Nest cavity 13 cm long and 14 cm wide, the top and the back consisting of pieces of cracked rock produced by road construction (Fig. 6, **AA-11**). Cavity lined with abundant fallen leaves, grasses and mosses. Outer cover thick. Wax envelope absent. Nest mass 9×7×5.4 (h) cm, approximately of the form of a slightly depressed sphere. The colony was transferred and reared till August 9.

Population: At nest removal foundress + 26 *W* and 24 batches as given in Table 9. After transfer in an observation box, the foundress survived till July 1

Table 9. Batch composition in *B. ardens ardens* Nest **AA-11** (Compiled on July 26 after final emergence from batches produced by foundress) (n/m=egg cells $n\sim m$ built in contiguity, *=parasitized by *Melittobia*, (n)=number of attacked cocoons)

Batch No.	Notes on stage and indiv. no. at nest removal, etc.	No. cocoons				No. failed to emerge
		Total	*W*	*Q*	*M*	
1	B 1∼10, earlier ones post-emergence, later ones	9	9			
2	with *A* or *P*.	13	13			
3		14	13	1		
4		6		6		
5		7	2	5		
6		7	1	6		
7		7	2	5		
8		8	2	6		
9		10	3	7		1 *W*
10	7 spinning larvae	6		6		
11	8 〃 〃	7		3	4	
12	7 〃 〃	7		5	2	
13	Larval cell	9		6	3	1 *Q**
14	〃 destroyed after transfer in observation box					
15	Egg cells, partly damaged at nest removal.	2		2		
16	Some larvae eliminated later. Probably each batch is composite, by fusion of 3∼4 egg cells	4		2	2	1 *Q**, 1 *M**
17/20	Egg cells, partly damaged and contents eaten, later 9 *L* removed	15		7	8	1 *Q**, 1 *M*
21	Egg cell (3 *E*), contiguous with 3 other pollen primed but not laid cells (Fig. 13, D)	Artificially removed				
22/24	These and subsequent cells built after nest transference, always 2∼4 cells in contiguity	7		3	4	1 *Q**, 1 *M**
25/26		9		3	6	
27/30	*LL* partly removed	19		8	11	1 *Q**, 3 *M**(2)
31/34	*LL* and *EE* partly removed	13		5	8	1 *M**
35/37	Cell 36 built by new *Q*, all eggs eaten by foundress (?)	12		8	4	4 *Q**(3), 2 *M**(1)
38/40	Hidden by B 27/30, failed to grow					
41/42		7		7		7 *Q**(4)
Total		198	45	101	52	1 *W*, 16 *Q*, 9 *M*

and produced in total 42 batches, from which many new *QQ* emerged. Some of these new *QQ* and some laying workers built many egg cells. Most of these cells (=batches W) were destroyed or the eggs were eaten as follows (x=hatched but all larvae not spun cocoons. In other batches, too, only some larvae attained cocoon stage. n *E*=number of eggs, unknown if unmentioned. n_1/n_2 in parentheses= number of larvae spinning cocoon/number of males emerged. *=some immatures parasitized by *Melittobia*): W 1(3, x), 2(x), 3/6 (11*//4), 7/9(3*//0), 10/11(1//0), 12/15 (6*//3), 16/18(x), 19/20(19=x, 20=1//0), 21/25 (18*//0, Fig. 13, F), 26+27+31 (?/

4*E*/4*E*, x), 28/29 (1*E*/1*E*, *x*), 30+32 (4*E*/?, hidden by W 21/25, undeveloped), 33 (4*E*, all eaten), 34/36 (4*E*/3*W*, partly eaten/2*E*, x). From these batches 40 cocoons were produced but only 7 *M* emerged and 13 *P* or *Pr* were parasitized by *Melittobia*.

Colony conditions: The colony is remarkable by the production of many *QQ*, considering relatively small size. Among batches built by the foundress, the number of *Q* cocoons exceeded those of *M*+*W*. The numbers successfully emerged are 44 *W*+85 *Q*+53 *M*, with 7 *M* by new queens and laying workers.

Miscellaneous notes: At nest removal there were 5 honey pots and 3 pollen pots at nest periphery (Fig. 13, A). No parasite and dead adult were found in the nest. Some other characteristics are enumerated (*=those more or less common to other nests): 1)* Nest mass is very compact (Fig. 13, A~C), not involving empty space since early stage. 2)* Most egg cells, built either by foundress or by laying workers, are in contiguity, forming a spheric group of 2~4 cells, not arranged linearly as in some worker built cells in *Bombus* s. str. (cf. Fig. 11, B). 3) All examined egg cells laid by the queen are primed with pollen. Further in B 22/24, egg cells

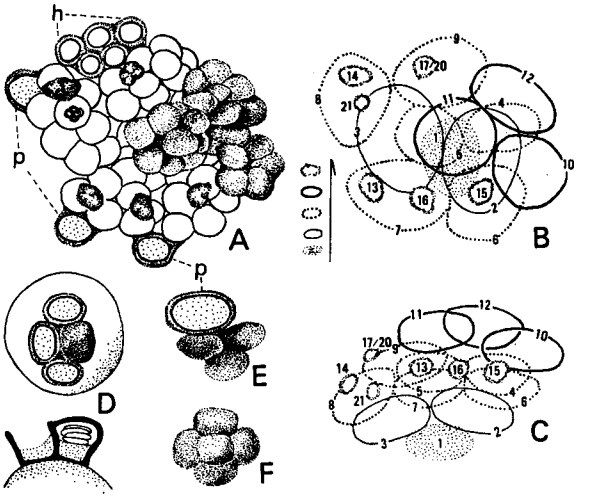

Fig. 13. *B. ardens ardens* Nest **AA-11.** A. Horizontal view (h=honey pot, p=pollen pot); B,C. Batch arrangement, horizontal and vertical views; D. Batch 21=egg cells, built contiguously with other three cells primed with pollen but before oviposition; E. Batches 22~24. Egg cells attached to the pollen pot; F. Batches W-21~25. Five egg cells built in contact.

were built by a pollen pot (Fig. 13, E, cf. also AS-1). Many other cells were also built by or on pollen pots. 4)* By this peculiar cell arrangment, many if not all batches distinguished in Table 9 after cocoon spinning should be composite ones. This trait and compact nest mass make distinction of real bacthes difficult. 5)

Egg cells are 6~7×6×7 (h) mm, built either on tops or at niches of postspinning cocoons. Worker built cells are variable but generally smaller than queen ones, and most eggs laid regularly, probably due to the small number of laying workers and no quarrelling among them.

In this nest many new *QQ* produced since B 3 participated in foraging and other tasks, and even in oviposition. The details are described elsewhere. It is possible that they virtually served as workers, though they were as large as the foundress. Phenomenally this resembles well the polyergism among queens in *B.* (*Fervidobombus*) *morio* (Garofalo 1976).

Bombus (*Pyrobombus*) *ardens sakagamii* (Tkalců) (=AS)

This form is widespread in Hokkaido but rather sporadic anywhere. The females, especially queens, are isochromic with *B.* (*B.*) *hypocrita sapporoensis*. Only one nest has so far been taken.

AS-1 (Fig. 14). Maruyama Park, Sapporo, June 25, 1976, taken by Messers. Sk. Yamane, M. Ito, S. Takahashi and S.F.S. In a cavity below stone steps leading to a monument built at margin of a *Cryptomeria* stand. Nest cavity surrounded by stones (Fig. 6, AS-1), 20×15×18(h) cm, communicated with the outside through another small cavity. Entrance hole 6 mm wide. Nest including outer cover 12× 12×9(h) cm, nest mass 8×8×6(h) cm, only partly covered with wax envelope, leaves below nest mass tightly fixed with wax. Cocoons bright yellow, wax dark brown, slightly paler than in **Dn-1.** Only a slight sign of attack at nest removal.

Population: Foundress (very old, Fig. 14, left), 25~30 foragers, some *MM* and some house bees (Exact number not determined), 1 *Wd* on nest bottom. The nest was transferred in a box but no particular observation was made. Sexuals gradually left the nest. New *QQ* did not participate in any tasks. At nest removal there were 8 egg cells and 208 cocoons. Batch composition was not studied. Contents and diameters of cocoons were studied after the disappearance of all adults on July 10 (Table 10).

Table 10. Contents and diameter of cocoons in *B. ardens sakagamii* Nest **AS-1**

Contents	Cocoon diameter (mm)							Total
	5	6	7	8	9	10	12	
Vacated		14	43	94	9		3	163
With honey		1	3	10		1	5	20
With pollen						1		1
With dead								
Aw			1					1
Am			5					5
Pq							2	2
Pr	3	7	4	2				16
Total	3	22	56	106	9	2	10	208

Colony conditions: At the end of the climax at nest removal, producing both *QQ* and *MM*. Percentage ratio of queen cocoons/total cocoons (10/208)=4.8%, ratio in emergence (184/208)=88.5%. Mortality in small cocoons is remarkable, only 60% of cocoons 5~6 mm in diameter produced adults.

Miscellaneous notes: 1) As in **AA-11**, nest mass was very compact, involving no empty space and separation of batches was impossible. Batch arrangement could be regarded as Type II by Wagner-Weyrauch. 2) One honey containing cocoon had wax overgrowth as long as its own length. Five tubular empty pots, 8 mm wide and 2.5~3.8 mm high (Fig. 14) were built at nest periphery, the bases of which were connected to a double-walled wax lamella, forming the side part of wax envelope. 3) All egg cells were built on the tops of the cocoons and mostly in contiguity (2, 2, 3, 1). A single solitary egg cell was built by a pot-like construct (Fig. 14), built on the top of a cocoon, certainly comparable to the pollen pot by B 22/24 in **AA-11** (Fig. 13, E). 4) All egg cells were open and empty, probably before pollen priming. The bottoms of some ones were not lined with wax, exposing cocoons.

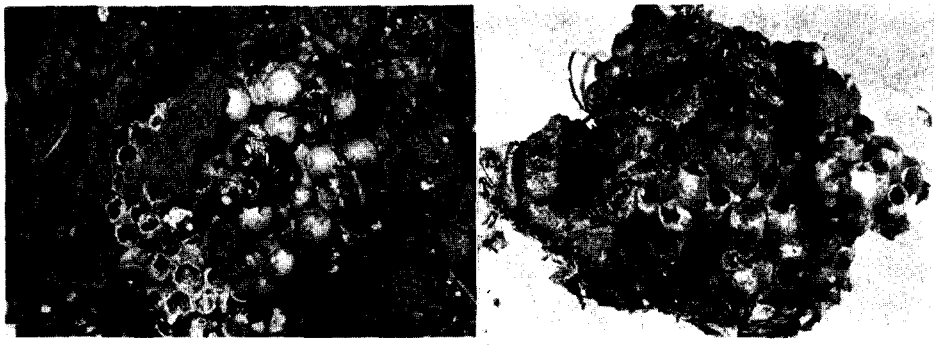

Fig. 14. *B. ardens sakagamii* Nest **AS-1.** Left. Horizontal view, photo at nest removal. Foundress queen at center, pollen pot attaching to an open egg cell below, wax cylinders left top, a male right top; Right. Oblique view, wax cylinder at left.

Discussions

In a previous paper, one of us (S.F.S.) reviewed various bionomic characters of bumblebees and criticized incomplete documentation in earlier records (Sakagami 1976). This criticism should be turned to many of our own records which have been taken for many years with variable accuracy. Remarks and discussions on some characters and related features are given below, approximately following the order of items enumerated by Sakagami (1976). Citations of other papers are limited to the minimum. First of all, here must be mentioned that our knowledge on Japanese bumblebees is poorest on three aspects, inicial nests before emergence

of workers, extranidal behavior of sexuals and hibernation, on which we have virtually no information.

1. Habitat preference

The primary climax vegetation of Japan is the forests, and most Japanese bumblebee forms should be more or less hylophilous. This is supported by their rapid decrease in and near Sapporo in parallel with intensified land development. Exceptions are *B. d. deuteronymus* and *B. pseudobaicalensis* in Hokkaido. In deforested areas these two forms outnumber all others. The high altitude forms are *B.* (*Pyrobombus*) *beaticola moshkarareppus* in Hokkaido and *B.* (*P.*) *b. beaticola*, *B.* (*Diversobombus*) *ussurensis* and *B.* (*Megabombus*) *consobrinus wittenburgi* (followed by *B.* (*Thoracobombus*) *h. honshuensis* in Honshu. Vertical distribution in central Hokkaido was given by Sakagami and Ishikawa (1969, Table 6). In Tochigi Pref., central Honshu, habitat preference and vertical distribution of various forms are approximately as follows:

	Habitat preferences	Vertical distribution (alt. m)
B. ignitus	Lowland rural areas to mountain outskirts	to 300~350
B. diversus and *B. ardens*	Lowlands adjacent to mountain outskirts to mountain forests, not deeply penetrating to rural openlands	to 1,000~1,500
B. hypocrita	Forests in mountain outskirts, both in valleys and ridges	350~2,000
B. honshuensis	Typically mountainous, not decending to mountain outskirts	500~2,000
B. consobrinus	Typically mountainous and sporadic, mainly in valleys, not in ridges	700~
B. ussurensis	Typically mountainous, very rare	700~
B. beaticola	Typically alpine, both below and above timber line	1,000~

2. Nest site preference

All recorded nests of *Thoracobombus* (nine authentic records and many other not well documented ones) have been found on the ground surface as in many consubgeneric species in Europe. These nests were found in the places where the undergrowth and litter layer relatively well developed, but not within real heaps of plant matter.

In all other forms nests were found in more or less concealed cavities, mostly being underground:

	Above-ground	Heaps of plant matter	Spaces between stones, under stone, shallow underground cavity (to ±15 cm)	Underground (cm) 20~30	~40	~50 or more	depth unknown
beaticola			1				
ardens	2	2	9	3	1		1
diversus	2	1	3	8	1	3	5
ignitus			2	4	3	1	
hypocrita				2	1		

All nests of two species of *Bombus* s. str. were underground as in other consubgeneric species. The same tendency is seen in *B. diversus* but less strictly. *B. ardens* seems plastic in site preference as in *B.* (*P.*) *pratorum* in Europe.

3. Nest defense

Few reliable data exist on the nest entrance camouflage, but **DD-6** possessed such. Constriction of entrance in **HS-1** is also regarded as a similar case. As to aggressiveness exhibited at nest removal. most observed forms are considered mild-tempted. Some workers flew to the persons but even in large nests no severe attack was experienced. The upside down defensive posture was exhibited by all precisely observed forms (*B. a. ardens*, *B. d. deuteronymus*, *B. d. diversus*, *B. d. tersatus*, *B. h. hypocrita*, *B. h. sapporoensis*, *B. ignitus*), and ejection of feces by *B. h. sapporoensis*, but regurgitation of honey in no forms. Specific difference seems subtle even if occurs. Possibly *B. diversus* is relatively mild even in large nests. Aggressiveness of *Bombus* s. str. has repeatedly been recorded. But **HS-1** was rather mild. In other nests **Ig-4** was relatively aggressive and **DD-13** also showed aggressiveness. These were large colonies containing many fresh house bees being ready to excite. Although more observations are required, the persistence of attack in large colonies may be ordered *ignitus*>*hypocrita*=*diversus*>*ardens*.

4. Egg cell

Although the available data are yet insufficient, egg cells in all observed nests of *Thoracobombus* were relatively flat, mostly built at niches between cocoons containing pupae or post-spinning larvae. Egg cells of *B. diversus*, *ardens*, *ignitus* and *hypocrita* were relatively tall, built more on the tops of cocoons with young pupae or postspinning larvae, in *B. diversus* sometimes also on those containing spinning larvae. Katayama (1965~'74) mentioned that egg cells of *B. ignitus* and *h. hypocrita* were often built in contiguity on the same cocoon, or even fused, while those of *B. d. diversus* were usually built isolately. But egg cells in two nests of *B. d. tersatus* (**DT-1, 2**) were mostly built in contiguity. These cells could be worker built. But in *B. ignitus* and *B. h. hypocrita*, even queen built cells tend to form a cluster or string (Katayama 1971, '74). In these two species the

number of eggs is variable and the orientation of eggs is irregular in worker built and laid cells. The same trait was observed in **DD-13** in the nest box (Katayama, unpubl.) and is expected in some other species, but was not seen in **DT-1, 2,** despite some cells, especially those in **DT-1**, must have been worker built. In *B. a. ardens* and probably *B. a. sakagamii*, building several egg cells in contiguity seems a rule by both queen and worker (**AA-10, 11**, AS-1). One to five, mostly 2~4 cells are built in contact, forming a spherical mass, not a string as often the case in *Bombus* s. str. (Figs. 10, 11 B). In this case real batches (p. 92) may be very difficult to determine (cf. 132).

Another interesting feature is pollen priming in egg cells, confirmed in two carefully examined nests of *B. a. ardens* (**AA-10, 11**) and in a single nest of *B. d. tersatus* (**DT-2**), but not in other forms. Pollen priming is known since Sladen (1912) and has been recorded in some species of *Pyrobombus*, *Megabombus*, *Subterraneobombus* and *Alpigenobombus*. Nevertheless, no precise observation on priming behavior has been described. Observations with **AA-11** are summarized: 1) Each cell is mostly built by several workers and the queen carefully rearranges the cell prior to oviposition. 2) Several cells forming a cluster are built either successively or synchronously according to the colony conditions and laying ability of the queen. 3) Completed cells do not receive eggs soon but are left mostly for several hours to one day. 4) During this time the cell receive pollen deposit by a few foragers. 5) After the pollen layer attained about 1/3 of cell depth, the queen manipulates pollen mass, rearranging the cell prior to oviposition. Two to three hours after, she oviposits in it and soon closes the orifice by herself. 6) Cells forming a group are primed either successively or synchronously and oviposited and closed successively.

Sakagami and Zucchi (1965) characterized oviposition behavior in bumblebees as a continuous activity by the queen or, though more erratically, by the laying worker, forming a chain, collection of material-building-oviposition-operculation, sharply contrasting to that in honeybees and stingless bees (cf. also Sakagami and Zucchi 1974, p. 411). In *B. ardens* this chain is broken by intervention of food provisioning lasting several hours, i.e. the sequence is just comparable to that found in *Eulaema nigrita* (Zucchi et al. 1969). Feeding the larvae through pockets is often regarded as more primitive than direct feeding, assuming the change from mass provisioning to progressive provisioning as a trend general to Aculeata. On the same basis, however, pollen priming can be considered more primitive, because preparation of feeding pocket involves itself a specialization. In this connection it must be stressed that pollen priming is found rather sporadically in several subgenera, not well corresponding to the classification based upon morphology as in case of pocket makers versus non-pocket makers (=pollen storers). The exceptional appearance of pollen priming in *B. diversus* (**DT-2**) is also noteworthy.

5. Feeding pockets

Feeding pockets were confirmed in *B. schrencki*, *pseudobaicalensis*, *deuteronymus* and *diversus*, all belonging to *Odontobombus* and biologically to pocket makers. Pockets were directed laterally in **Dn-1**, but mostly upwards in all other precisely recorded cases. No positive evidence on regular destruction followed by reconstruction of pockets (Weyrauch 1934) was obtained and actually such was not observed in **DD-6, 7, 8,** (Katayama 1966 a).

In *B. diversus* one larval cell often had more than one pocket (Katayama 1966 **DD-7, 8** and **DT-2**). A pocket common to two cells was found in **DD-12**. There is a controversy of observations as to feeding of sexual larvae in *Fervidobombus*, direct feeding as in non-pocket makers were recorded in some species while pockets were described in others (Sakagami 1976, p. 405, 407). In *B. atratus* the pocket is present but sexual larvae receive additional food after disappearance of pocket through continuously opened orifice, just as in a non-pocket marker *B. h. hypocrita* (Katayama 1975). As suggested in Katayama (1975) seemingly this additional feeding does not affect the mechanism of caste determination but accelerate size difference of two castes. At least in *Subterraneobombus* (Hobbs 1966 b) and *B.* (*Thoracobombus*) *pascuorum* (Cumber 1949) sexuals are also reared through pockets. In the present study, pockets for sexual batches were found in **Dn-1, DD-C, 12, 13, DT-1, 2** and certainly for queen batches in **DD-C** and **DT-2.** It is unknown whether additional feeding occurs or not in these forms. Another, hitherto unnoticed problem is how larvae in mixed batches are fed.

In **DT-1** all pockets were separated from the larval cell proper by a wax wall, the feature so far unrecorded in pocket makers (Fig. 7). In **AA-11** (Fig. 13, E) egg cells were built by a pollen pot. A similar structure was also found in **AS-1** (Fig. 14). Hobbs (1965 b) recorded pollen cylinders attached to larval cells in *B.* (*Cullumanobombus*) *rufocinctus*. Haas (1962) described, as an anomalous case, pollen pots built by larval cells of *B.* (*Pyrobombus*) *hypnorum*. Precise studies of these presumably optional structures as well as pollen priming (p. 129) may enlighten the evolution of brood rearing habits in bumblebees.

6. Batch arrangement

It has been said that cocoons forming a batch fuse more tightly in pocket makers than in non-pocket makers (=pollen storers), and each batch is more easily recognized in the former (Sakagami 1976, pp. 408~409). In our nests, too, batch recognition was in general easier in *Thoracobombus* and *Diversobombus* than in *Pyrobombus* and *Bombus* s. str. But causes to make batch distinction difficult should be variable: 1) Loose connection of cocoons. This seems characteristic to *Bombus* s. str. as pointed out by some authors. In **HS-1, HH-2, Ig-9,** cocoons containing spinning larvae easily detached from the cluster. 2) Contiguous building of egg cells. This may be likely in *B. hypocrita*, *B. ignitus* and particularly in *B. ardens*. In the last species distinction of batches must be imposible in large

nests (cf. **AS-1** and **AA-7, 8,** Katayama 1964), unless daily checks are made. Precise records are wanted for cocoon clustering in *Bombias*, which does not have batches by our definition (p. 94) as each cell receives a single egg (Sakagami 1976, p. 409). 3) Absence of feeding pockets. According to Weyrauch (1934) pockets function to lead the expansion of nests without collision among growing batches. This factor seems less important than stressed by him (Sakagami et al. 1967), but cannot be ignored in future studies. 4) Colony size. As stated below, batch arrangement is clearer in small colonies, which also make distinction of batches easy.

In connection with batch distinction, types of batch arrangement distinguished by Wagner (1907) and Weyrauch are referred to (Sakagami 1976, p. 409). A defect of their system is that it does not consider colony stages. Hobbs (1964 b$\sim$1968) clarified that the second and a few subsequent batches were built upon the ridges of the first batch in all subgenera studied by him, including *Bombus* s. str. This means that in any species initial nests should take some rosette like plan. Even in *B. ignitus* and *B.h. hypocrita*, such plan is clear in earlier nests (Fig. 9), never taking type I (Planloses Durcheinander der Einzelteile) designated by the cited authors for their European consubgeners (*B. terrestris* and *B. lucorum*). But it is also certain that invert-pyramid arrangement as in Fig. 9 could hardly be kept in larger nests when no active adjustment is taken by workers. Consequently batch arrangement may be regular in earlier nests than in later ones in any species. This assumption is in part supported by the fact that types III$\sim$V by Wagner-Weyrauch with regular arrangement are all represented by *Thoracobombus*, the colonies of which are usually small.

However, some species or group specificities do occur. Among four nests of *Thoracobombus* studied by us (Fig. 1$\sim$4), rosette arranegment was clearer in two smaller nests (**SA-1, Ps-1**) than larger ones (**Dn-1, SA-2**) in which the top was covered by later batches. But even in these nests, the nest center contained an unoccupied space. Such centrifugal tendency was less distinct in nests of other species. Particularly nests of *B. ardens* (**AS-1, AA-11**) was very compact with no ample intranidal spaces, suggesting some group specificities. However, even in *Thoracobombus*, the nest mass is not a product of mechanical up- and sideward expansion. In **SA-1, 2** and **Ps-1** some dislocated batches of vacated coccoons were found on the nest bottom. These are certainly quite old batches and indicate active rearrangement since early colony stages. In larger nests of *B. diversus* such dislocation should be more frequent and in those of *Bombus* s. str., recombination of batches may accelerate irregular arrangement. In *B. d. tersatus*, **DT-2** (Fig. 8), the smaller nest, still retains a centrifugal tendency, but **DT-1** (Fig. 7) already little. Comparing **DT-1** and **HS-1** (Fig. 10), no virtual difference is detected though arrangement is never completely "planlos". Probably it is futile to seek clear batch arrangement for nests of this size or larger ones.

7. Batch size

In introduction (p. 92) "batch" was defined as the group of immatures born in the same cell. But for post-spinning stages batches were actually distinguished as group of cocoons forming a cluster. Distribution of batch sizes in some nests is summarized in Table 11. The table does not include **AA-11,** because in *B. ardens* many if not all batches separated as clusters seem composite due to the specific trait of building egg cells in contiguity. Instead, the result obtained for a laboratory reared colony of Neotropical species *B. (Fervidobombus) atratus* was cited from Sakagami et al. (1967). How these distributions deviate from real batch size is

Table 11. Frequency distribution of batch size in some studied nests. C=cocoons, L=larval cells, E=egg cells, W=cells built and laid by *WW*, V=vacated cocoons (probably mostly worker cocoons), X=mixed batch, M=male batch. Data on *B. (Fervidobombus) atratus* cited from Sakagami et al. 1967.

Batch size	SA-1			SA-2	Ps-1	DD						DT-1			DT-2			Ig-9			HH-1		HH-2			HS-1			*B. atratus*		
						10 11		12		13																						
	C	L	E	C	C	C	C	C	L	C	W	C	L	E	C	L	E	V	X	M	V	M	V	X	M	C	L	E	C	L	E
1	1							2		9								1		5			1		1		5					
2										4			1	1						5			1	1			2					
3						1		1		2	2		1							3			2		4		2					
4										3		3	4	1				3		5		2	1		2	3	1					
5				1				1		3		7	1	6	1			2		3			1			2		1				
6						1	1	5		1	1	9		5	1			9	2	7	5		14	3	3	5	1		2			
7	2			5	3	4	1	4		2	2	8	1	3	3	2	3	7	2	4	2		9	3		9	1		6	2	3	
8	1			2		3	1	6		1		4		2	3	1	1	9	1	6	2	1				9			9	4	7	
9				5		3	2	6				2		3	1	1		5	1	2	3			2		3			10	5	2	
10	3			4			1	1		5		5			1		3	2				3	1			7					2
11	1			2	3		2	8		1	1	4			2			1			3	2				3					
12					1		1	8		3		8			4					1	3		1									
13				2				5		7		1			1						2	1				1						
14		1		1	1		1	1		7		4			1						3					2						
15										4		3						2		1												
16								1		7		3			2																	
17								1		7		4			1																	
18								1		6		3			1																	
19										3													2									
20										4		3																				
21																							1			1						
22												1																				
23																							1									
24												3																				
26																						1				1						
27																											1					
28																										1						
31																					1											
43																											1					

unknown. Probable factors causing such deviation and related comments are given below.

1) Peculiarity of cells built upon the first egg cell: Hobbs (1964 b～1968) and Alford (1970) clarified peculiarities of the first egg cell built by the foundress to subsequent cells in structure and orientation of eggs (Sakagami 1976, pp. 397～400). A few subsequent cells are built on the ridges of the first cell usually in contiguity. Hobbs showed difference of batch sizes between the first cell and those built upon it (=the second layer batches):

Subgenus species	Batch size	
	first cell	cells on the first cell
Alpinobombus balteatus	11 (7～21)	10
Pyrobombus spp.	8～9 (pupae)	3～4
Bombus occidentalis	8.6±0.5+1～2	4.2
Fervidobombus californicus	10	2～7
F. fervidus	8	3～4
Subterraneobombus appositus	13±3 (pupae) to 24	3.6±1.2

In all species except *B. balteatus* size of second layer batches is smaller than in the first cell and also smaller than in later batches (mostly 6～10 or more). If this tendency is a rule, we should find in nests slightly after initial stage some small clusters of vacated cocoons near the nest bottom, provided there was no later fusion of batches and no active dislocation of such clusters. But these two factors must usually be in operation, as such small batches were not found in our nests. Fusion of the second layer batches may be especially easier as these are built in contiguity. This point could be solved only by periodical inspections of nests since earlier stage. If later egg cells are also frequently built in contiguity as in *B. ardens*, precise distinction of real batches becomes impossible or meaningless. In such case, it might be better to regard one cell group as one batch.

2) Real batch size and additional ovipositions: Precise observations of oviposition behavior are scarce. Number of eggs laid in a cell in these records are: Sakagami and Zucchi (1965, *B. atratus*, 8 eggs/4 times, 9/2), Katayama (1971, *B. ignitus*, 8/1, 9/3, 10/2; 1974;, *B. hypocrita*, 7/1, 8/2, 9/1, 10/1), Garofalo (1976, *B. morio*, 11/3, 12/4, 13/2, 14/2, 15/1, m=12.5), all being higher than size of the second layer batches cited above. It is possible that queen laying rate increases in parallel with colony development. It will be expressed by either larger batch size or shorter intervals between oviposition processes. Both seem possible and the first item seems more important from the result by Katayama (1966 a, *B. d. diversus*, **DD-8**), but there are no precise data which show two parameters separately.

Another factor affecting real batch size is additional ovipositions in an egg cell once oviposited and sealed. This is reported not only for the first batch (Hobbs, Alford, op. cit., K.W. Richards 1973, cf. Sakagami 1976, p. 398) but also for later cells (e.g. Sladen 1912, *B. lapidarius*; Meidell 1934, *B. agrorum bicolor*). Such additional ovipositions in later cells were confirmed in none of direct observations cited

above. Possibly this appears mainly by senescence of the foundress, often accompanied with development of laying workers. If such additional ovipositions are frequent, real batch size cannot be determined with precision even by means of direct observation.

3) Brood mortality: Batch sizes determined by direct observation of ovipositions and by separation of clustered cocoons should deviate by mortality during egg and larval stages. Brian (1951) recorded a high mortality in two colonies of *B.* (*Thoracobombus*) *pascuorum* (64 and 69%), mostly during egg to early larval stages, and assumed an intensive cannibalism. One of us (E.K.) also observed in some rearing colonies (**Ig-9, HH-2, AA-11**) active removal of larvae at the peak of queen ovipositions. No such high mortality was found in a laboratory colony of *B. atratus* (Sakagami et al. 1967. Compare distribution of batch sizes among cocoons, larvae and eggs cited in Table 11). Such removal of larvae might occur in natural nests in adverse conditions. Diverse instances may fluctuate between these two extremes.

Percentage ratios of post-spinning larvae, prepupae and pupae dead in cocoons to total vacated cocoons and to total cocoons are presented in Table 12. In the colony of *B. atratus* cited above one of us (S.F.S.) never observed removal of dead immatures from cocoons. This is also true to all colonies of Japanese forms reared by E.K. except **AA-11**, in which some cocoons parasitized by *Melittobia* were opened by workers after emergence of several *Melittobia* adults, and a dead pupa was removed from one cocoon. If this is a rule to bumblebees, or at least prevalent,

Table 12. Ratio of immatures dead in cocoons to total cocoons produced in some nests (*=reared in observation box)

Nest	No. cocoons			% mortality	
	A with dead	B vacated	C total	A/B	A/C
SA-1	8	27	63	29.6	12.7
2	0	203	203	0.0	0.0
Dn-1	15	61	134	24.6	11.2
DD-12	1	451	489	0.2	0.2
13	7	761	860	0.9	0.8
DT-1	4	637	835	0.6	0.5
2	3	210	239	1.4	1.2
***Ig-9**					
W batch	1	316	317	0.3	0.3
M "	23	235	258	9.8	8.9
HH-1	0	298	340	0.0	0.0
***2**					
W batch	5	280	285	1.8	1.7
MQ "	2	79	81	2.5	2.5
HS-1	3	291	433	1.0	0.7
***AA-11**	59	179	238	32.9	24.8
AS-1	24	184	208	13.0	11.5

the figures in the table are regarded as prepupal and pupal mortalities, which are low or very low. Perhaps stages within cocoons are the safest during life cycle like as in honeybees (Fukuda and Sakagami 1968). In this case only mortality before cocoon-spinning is important for deviation between real and counted batch sizes.

4) Instability at later stages: At later colony stages senescence of the foundress and appearance of laying workers disturb regular oviposition sequence. Mean batch size in laying workers at a given oviposition process is smaller than in the foundress (Table 11, **DD-13, Ig-9**). But common use of the same egg cell by several workers (Katayama 1974, p. 432) and frequent oophagy make batch size irregular as shown by erratic distributions of batch size in larval and egg cells (Table 11, **SA-1, DT-1, HS-1**). Such conflicts must disturb even successful development of post-feeding larvae as suggested by higher pupal mortality in sexual batches than worker batches (Table 12, **Ig-9, HH-1**). Certainly the last phase of colony cycle must separately be considered with resepct to batch size.

Distributions of batch sizes in Table 11 are products of these diverse factors. Fluctuation is lowest in *B. atratus* which was observed under careful daily check and low brood mortality. In other nests, excluding apparently composite batches (those larger than 15~20), worker batches are on the average larger than eight, the number of ovarioles possessed by females. Probably some ovarioles supply more than one egg at a given oviposition process. Even admitting the presence of many composite batches, specific difference seems to occur. Possibly *B. diversus* produces larger batches than other forms like in some species of *Subterraneobombus* (Sakagami 1976, p. 436).

8. Food storage

Reliable estimation of the amount of food stored in bumblebee colonies is difficult, which is a serious obstacle to study colony development quantitatively. The numbers of cocoons used for food storage, wax storage pots, etc. in some nests are given in Table 13. At the present no definite statement can be made but the following comments will be suggestive for future studies: 1) Amount of food storage greatly varies from colony to colony. Some nest near the end of colony cycle (**Dn-1, DD-12**) had virtually no store, but others, e.g. **SA-1, 2, DT-1, 2, AS-1** still had a considerable reserve. 2) Although both honey and pollen are deposited in vacated cocoons, pollen is stored often in other receptacles, or even as amorphous mass, despite the presence of many empty cocoons. 3) Both pocket makers and nonpocket makers prepare wax pollen pots. It is possible that amount deposited in pots is larger in non-pocket makers. But even in pocket makers (**SA-1, DT-2**) more pollen can be deposited out of feeding pockets. This favors replacement of the term "pollen storers" used since Sladen (1912) by non-pocket makers (Sakagami 1976, p. 404). 4) Some long pollen pots in **HS-1** were covered with wax only at the tops, virtually changing to exposed pollen columns (Fig. 11, D; cf. also **DT-2**, Fig. 8, 4–2). Possibly wax cover can be removed and applied to

Table 13. Condition of stored

Nest	Total post-emergence cocoon	Honey stored in post-emergence cocoon			
		not wax coated	wax coated	closed	Total
Pocket makers					
SA-1	27	4	3		7
2	203	3	9	2	14
Dn-1	61	2			2
DD-D	311				102
12	451			2	2
DT-1	641	32	66	78	176
2	210		50	2	52
Non-pocket makers					
HH-1	298				143
2	66				50
HS-1	291	29	63		92
AA-11	34				34
AS-1	184				20

other purposes if necessary.

9. Wax envelope

In *B. diversus, hypocrita, ignitus* and *ardens* wax envelope below the outer plant cover was observed at least in some nests (*=incomplete): **DD-6, 12, DT-1, Ig-6*, 7, *9*, HH-1, 2*, HS-1, AA-C, AS-1*. DD-13, DT-2** and **AA-11** had no envelope and its presence or absence was not checked in other nests. In general development of wax envelope seems better in later stage nests and in nests with poor plant cover. On the other hand, all accurately recorded nests of *Thoracobombus* were devoid of wax envelope, which accords to the records in Europe since Sladen (1912, cf. Sakagami 1976, p. 412).

10. Size variations among females

Among winged social insects bumblebees exhibit the highest size variation in females (cf. Fig. 15, *Apis* and *Bombus*). Previous discussions on this aspect can be split in two closely related, yet different problems: 1) Whether size difference among workers shows any trend along colony development or not ? 2) Whether queens and workers are discontinuous in size or not ?

In some nests we measured diameter of each cocoon (Tables 1～3, 5～8). The order of batch sequence given by us would not exactly correspond to real sequence, and some cocoons must be those having issued males. But a general trend is obtainable from the tables. What inferred from these trends is that mean worker size sometimes increases parallel to colony development but sometimes not.

food in some studied nests

Pot		Pollen stored in			
honey	empty	cocoon	pot	amorph. mass	pocket
	1			2	1
		8+1			
	1		1		3
					2
	1				
	3				9
1	1		3	1	7
5			7		
3		4			
			12		
5			3		
	5	1			

Probably mean worker size reared by the foundress is smaller. Later, mean size may increase by improved food supply. But this factor is so unstable that easily masked by diverse environmental and colony conditions such as food storage, worker-larva ratio, etc. This may explain previous controversy on the relation between seasons and worker size, though some specific difference is plausible (Plowright and Jay 1968).

Another factor of probable importance is that bumblebees (except *Bombias*, cf. Hobbs 1965 a) are unique among winged social insects by abandonment of unit cell system. Resulting competition among batch mates for food must enhance size variation[1]. Occasional production of dwarf cocoons (cf. Tables 1~3, 5~8), usually located at the bottom of the batch and often lying horizontally, would be an outcome of such competition. A higher mortality in smaller cocoons in **AS-1** (Table 10) favors this assumption.

The queen-worker discontinuity in cocoon diameter is indistinct in **SA-2** and **Dn-1** (Tables 2, 3) but not in other forms. In some nests head width (=outer orbital distance) was measured for all adult females captured at nest removal and those emerged later. For *B. pseudobaicalensis*, the females of nests **Ps-1**, **Ps/SA-A**, **B** were used in combination. The results are presented in Fig. 15. Queen-worker discontinuity is clear in *B. hypocrita* and *B. diversus* but not in *B. pseudobaicalensis* and particularly *B. deuteronymus*. This corresponds well to the experience by one of us (S.F.S.) who often has had trouble to separate queens and large workers of *Thoracobombus* captured on flowers. The same tendency seems to occur in Europe (Løken 1973, cf. Sakagami 1976, p. 418). Previously it has been asserted that

1) It may be interesting to compare size variation in *Bombias* with other subgenera.

queen-worker discontinuity is greater in non-pocket makers than in pocket makers. This may be true as a general trend but obscures differences existing within each group. Röseler (1974) showed continuity in *B.* (*Pyrobombus*) *hypnorum* and discontinuity in *B.* (*Bombus*) *terrestris*, both being non-pocket makers. In Fig. 15 discontinuity in *B. diversus*, which is much clearer in fresh body weight (Fig. 16), is nearly as large as in *B. hypocrita*.

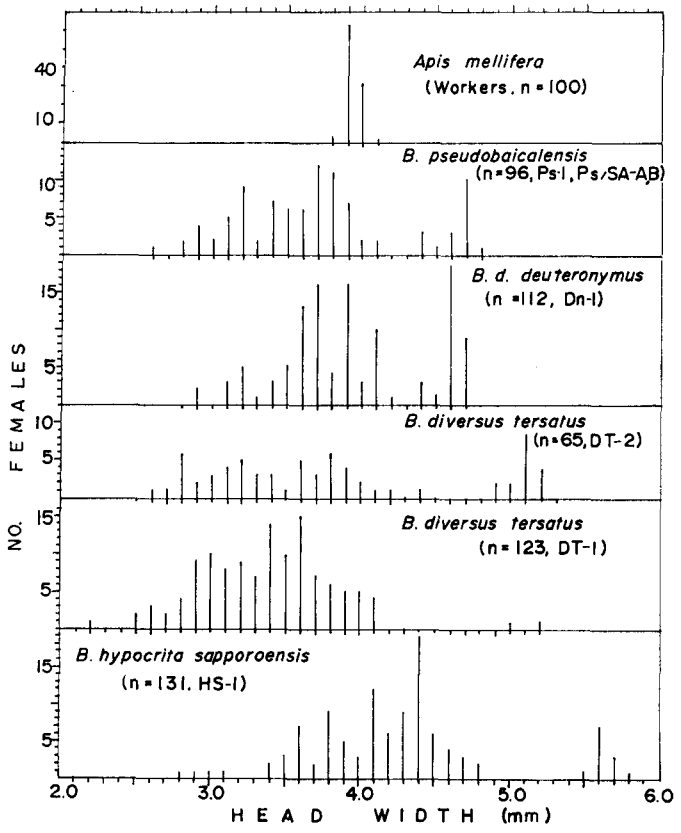

Fig. 15. Frequency distribution of female head width in some nests. A sample of worker honeybees at the top (n=sample size. Nest No. in parentheses).

11. Allometric trends in some metric characters

In some nests other metric characters were measured for all workers: Relation between head width and number of hamuli (Table 14), relations between upper maximum and lower interorbital distances, interocellar and ocelloccipital distances (Fig. 17) and malar length and width (Fig. 18). In all these comparisons,

discontinuity is again indistinct in *Thoracobombus*, especially in *B. deuteronymus*, in which the number of hamuli virtually does not differ between two castes.

All three relations in Figs. 17 and 18 change allometrically. But deviation from isometric line is specifically different, being *diversus*≫*pseudobaicalensis*> *deuteronymus*. The trend is clearest in ratio interocellar/ocellorbital distance, which may be the best index to express allometric change (Sakagami 1972, '75). Allometric trend in Fig. 18 is noteworthy, as it deals with one of the most important diagnostic characters in bumblebees. Difference between *B. d. deuteronymus* and *B. pseudobaicalensis* is clear in larger females but becomes smaller in smaller females.

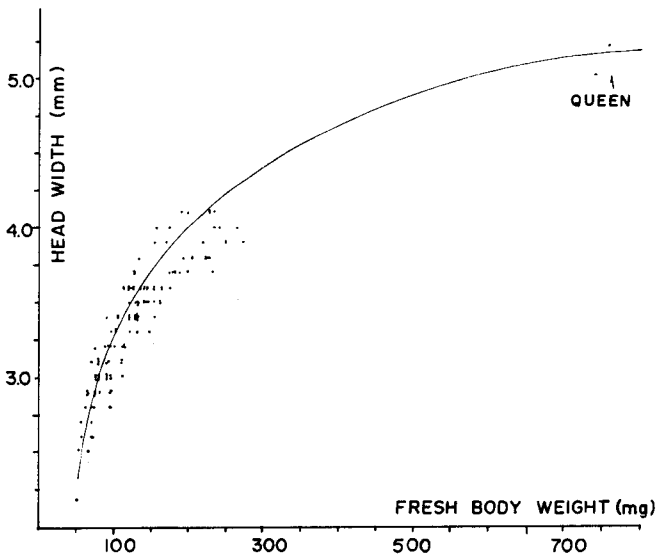

Fig 16. Relation between head width and fresh body weight (pollen loads excluded, crop weight included) in females of *B. diversus tersatus* Nest **DT-1.** Trend curve drawn by eye.

Queens of *B. diversus* have extremely long malar space but its dwarf workers have the ratio L/W nearly identical with that of *B. pseudobaicalensis* queens. Although yet not well worked out, some of these allometric trends can be used as characters diagnostic of species or supraspecies groups. Fig. 19 illustrates allometric differences between the largest and smallest females in *B. diversus*, **DT-2.** The differences are accompanied by changes of some non-metric characters. Labral tubercles (Fig. 19, G,H,I), epipygial tubercles and some other sculptural characters are clearest in queen but undeveloped in workers, especially in smaller ones. By these size-linked changes of female diagnostic characters, bumblebees sharply contrast with two highly eusocial sister groups, honeybees and stingless bees, in

Table 14. Relation between head width and no. hamuli in females of some studied nests

Form and nest	Head width (mm)	Number of hamuli (left wing)																		
		12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
B.d. deutero-nymus **Dn-1**	2.5~3.0			1																
	~3.5				4	3	8	2												
	~4.0				1	5	13	20	8	5										
	~4.5						2	3	3	4										
	~5.0							5	8	10	1									
B. pseudobai-calensis **Ps-1, Ps/SA-A, B**	2.5~3.0					2	2	2	2											
	~3.5						4	6	14	7										
	~4.0						1	5	10	13	8	1								
	~4.5							1	1	1	2	1								
	~5.0								1			9	2	1						
B.d. tersatus **DT-2**	2.5~3.0	1	4	3	2		1													
	~3.5				3	4	4	1												
	~4.0						5	4	4	5	2									
	~4.5									1	1									
	~5.0										1	2	1							
	~5.5									1	1	3	2	3	2					
B.h. sapporoensis **HS-1**	2.5~3.0				1				1		1									
	~3.5					1		2	1		1				1					
	~4.0					1		3	2	3	3	7	4	2	1					
	~4.5										10	7	19	10	4					
	~5.0											3	6	2						
	~5.5																			1
	~6.0													1	1	3	3	2		

which diagnostic characters are more differentiated in workers than in queens, whose "parasitic" lives must have brought degeneration of various characters.

12. Size- and age-linked polyergism in workers

Size variation in bumblebee workers is much larger than in honeybees (Fig. 15). The influence of size and age upon division of labor or polyergism in workers was analysed in some nests.

Relative age was determined by wear of wing tips and hair coat (I=intact, II=lightly worn, III=heavily worn). Workers were classified into house bees and foragers, the latter involving bees captured out of nests and those carrying trace of pollen loads on hind legs. There are two sources of observational errors. 1) Wing wear should be heavier in foragers than in the same-aged house bees. 2) Some workers captured within nests with no trace of pollen loads might be foragers.

The results (Table 15) tell three general trends: 1) Foragers are relatively old. 2) But this tendency is not clear. There are many young foragers. 3) Dwarf workers tend to stay in nests.

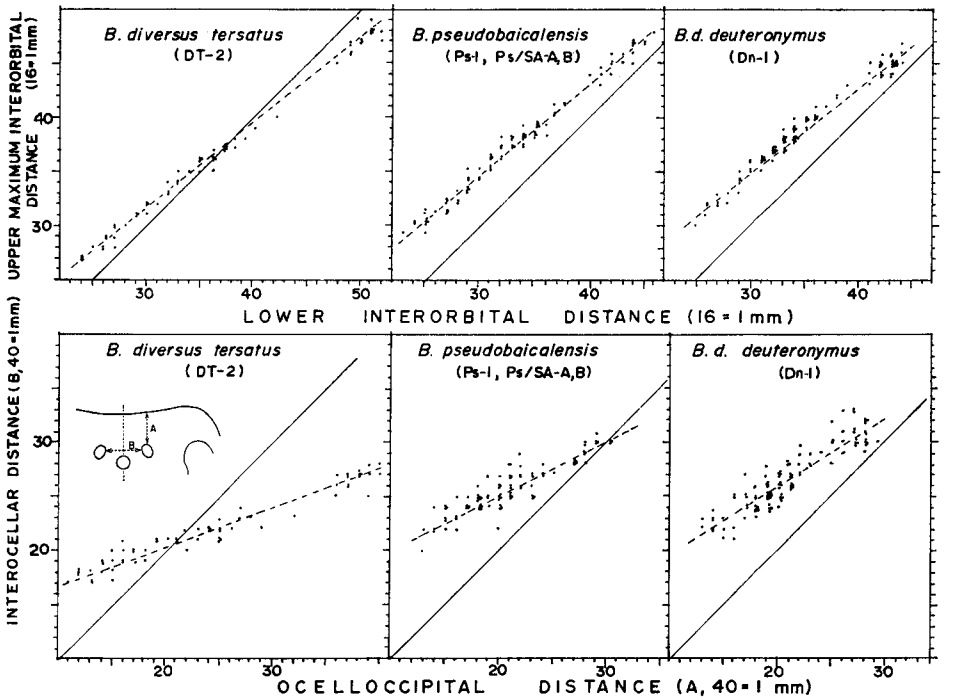

Fig. 17. Distribution of ratios upper maximum interorbital distance/lower interorbital distance and interocellar distance/ocelloccipital distance in females of some nests. Trend lines by eye.

The first trend is more or less common to most social insects in general, though less conspicuous in social wasps (Matsuura 1973). The second trend suggests an age-linked polyergism less acute than in honeybees and stingless bees, in which age sequence is intimately correlated with physiological conditions, especially with secretory glands, and participation in foraging takes place only after passing a prolonged household period (cf. Terada et al. 1975). The third trend also differs from polyergism in monomorphic workers of honeybees and stingless bees, rather resembling those in some polymorphic ants (Wilson 1971). The workers as small as those in the smallest groups of the studied nests are seldom captured on flowers. They must spend nearly entire life within nests (Sakagami and Zucchi 1965), just as dwarf workers of fungus-growing ants (cf. Goetsch 1934). As suggested in p. 137 such dwarfs would be a product of mal-nutrition. Yet selec-

tion to eliminate them has seemingly not operated in bumblebees, possibly by utility of dwarfs within nests, which contain inter-batch pathways much irregular than in combed nests of other winged social insects.

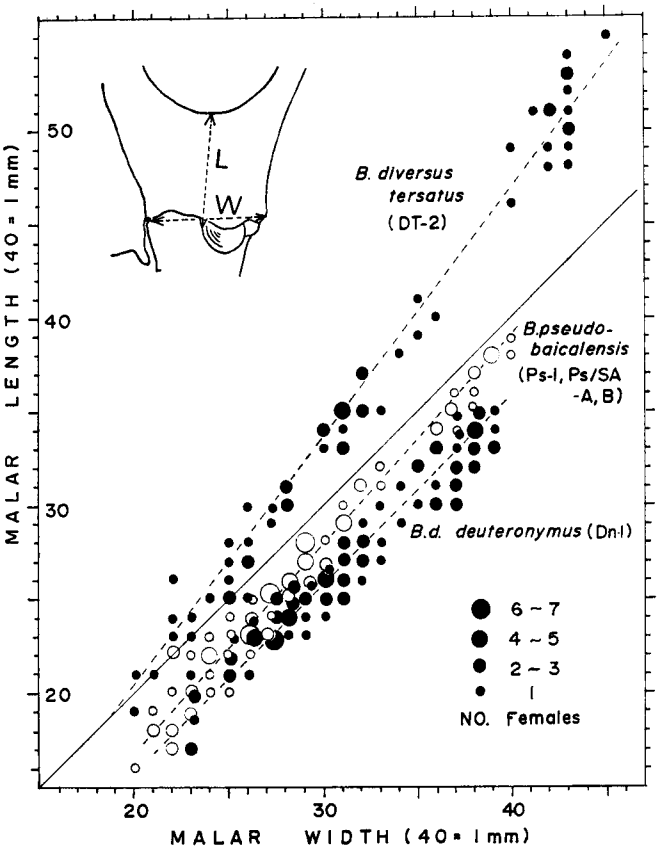

Fig. 18. Distribution of ratio malar length/width in females of some nests. Trend line by eye.

13. Colony size, production of sexuals, and laying workers

Table 16 presents the data on colony size in some studied nests which produced some sexual broods and those not produced sexuals but taken approximately on same dates or later in the same localities. It is difficult to find a reliable and easily obtainable parameter to compare colony size. We regard the total number of cocoons produced as such, because: 1) Bumblebee cocoons are resistant, rarely completely disintegrated even though partly torn. 2) Number of

cocoons can be determined either at nest removal or after being reared for some observations.

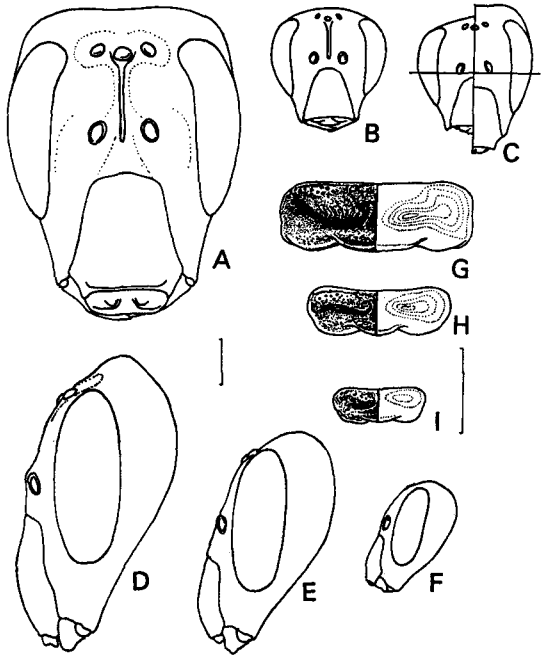

Fig. 19. Allometric change of head (A~F, small scale, 1 cm) and size-linked variation of labral sculpture (G~I, large scale, 1 cm) in females of *B. diversus tersatus* Nest **DT-2.** A~C. Head, frontal view, D~F. Head in profile, A,D, G=queen, E, H=large worker, B,I,F,=dwarf worker, C=Left as in B, right as in A but shown with reduced scale (head width at lower level of alveoli drawn equal to that of B).

Although the available data are scanty, climax nests of *Thoracobombus* are usually small. Some other climax nests not precisely recorded by S.F.S. hardly exceeded 200 cocoons. Among other species, *B. ardens* with short colony cycle (Fig. 20) has on the average smaller nests, though occasionally attaining 700 cocoons. The largest Japanese nest obtained is **Ig-4** with 1,300 cocoons. But probably the climax nests of *B. d. diversus* may be larger on the average, judging from its longer life cycle (Fig. 20), and probably larger mean batch size (Table 11).

It is known that some climax nests produce sexuals but others not, and in the former group, some produce both sexes while some only one sex (Free and Butler 1959). Many nests which did not produce sexuals should be mal-developed (cf. **SA-1**), but it is difficult to conclude the absence of male production, because: 1) Males and workers are difficult to distinguish by cocoons. 2) As males leave nests earlier and do not return more, their absence in nests does not necessarily

Table 15. Size- and age-linked worker polyergism in some nests

Form and nest	Head width (mm)	No. workers classified by tasks and relative age (I, II, III, young to old, newly emerged excluded)					
		House bees			Foragers		
		I	II	III	I	II	III
B. pseudobaicalensis **Ps-1**	3.2~3.3	1					
	3.4~3.5	5			1		
	3.6~3.7	2			2		1
	3.8~3.9	1			3	3	3
B. pseudobaicalensis **Ps/SA-B**	2.6~2.7	1					
	2.8~2.9	2	1				
	3.0~3.1	3					
	3.2~3.3	1	1		2	1	
	3.4~3.5				2	2	
	3.6~3.7					3	
	3.8~3.9					3	2
	4.0~4.1				1		
B.d. deuteronymus **Dn-1**	3.0~3.1	3					
	3.2~3.3	6					
	3.4~3.5	2		1	1	1	1
	3.6~3.7	7			2	5	5
	3.8~3.9	2			1	3	3
	4.0~4.1	1					1
B. diversus tersatus **DT-1**	2.2~2.3	1					
	2.4~2.5	1	1				
	2.6~2.7	2	2	1			
	2.8~2.9	4	8	1			
	3.0~3.1	16	3			1	
	3.2~3.3	10			4	1	1
	3.4~3.5	11	2		10	1	1
	3.6~3.7	7	1		7	4	
	3.8~3.9	7			1	4	2
	4.0~4.1	3			4	3	
B. diversus tersatus **DT-2**	2.6~2.7	1	1	3			
	2.8~2.9	2	3				
	3.0~3.1	3	3				
	3.2~3.3	2	2		3		
	3.4~3.5				1		
	3.6~3.7	2			4	2	
	3.8~3.9	3	1		5	1	1
	4.0~4.1				2		
	4.2~4.3	1					
	4.4~4.5				1		

mean that they were actually not produced. 3) Even in mal-developed nests, the appearance of laying workers may lead to male production, and separation of queen born and worker born males is not easy. It is of theoretical interest to know the queen/male ratio produced by a colony with respect to relative importance of queen and worker controls for production of sexuals (Trivers and Hare 1976). But from above difficulties it is not always easy to obtain reliable estimation of queen/male ratio for a particular colony, unless continuous record was taken as in **DD-13, Ig-9, HH-2, AA-11,** in which separation of three broods is clear (*=many worker born eggs were artificially removed or abandoned by workers).

	Queens	Queen born males	Worker born males
DD-13	0	14	81
Ig-9*	0	235	23
HH-2*	23	46	12
AA-11	101	52	40

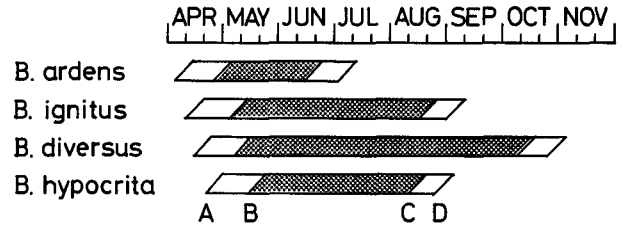

Fig. 20. Colony cycle of some bumblebee species in lowland and hilly areas in Tochigi Pref., central Japan. A=Nest foundation started; B=Worker emergence started; C=Emergence of sexuals started; D=Dissolution of colony started.

Consequently, the percentage ratio of queen cocoons to total cocoons is regarded as the most easily obtainable index of colony productivity, though for some subgenera, e.g. *Thoracobombus*, distinction of queen and non queen cocoons is often arbitrary (in the present study, cocoons 10 mm or more in diameter=queen cocoons). This ratio (Fig. 21) ranged from 0 to 37.5%, with an exceptional value of 42.4% in **AA-11**. Concerning the colonies which produced queens, the number of queen cocoons is roughly proportional to that of total cocoons. But it is noteworthy that many nests did not produce queens, despite some ones were fairly large (**DD-13, Ig-9**). Although more reliable data are required, queen production seems not simply be determined by colony size alone.

When both males and queens are produced, male production prior to queen is generally accepted (e.g. *B. pascuorum*, W-WM or M-(MQ)-Q, Free and Butler 1959). In our nests this sequence was not followed in some nests, **DT-1, HH-2** and probably **Ig-6, HS-1** and **AA-11**, with male production after issuing queens. In the first four nests, it is likely that this was caused by laying workers, but in

Table 16. Colony size and productivity of some studied nests (*=Examined

Taxon and nest	Date of census	Presence or not of foundress	No. workers	*M*
Thoracobombus				
SA-1	VIII 3	+	±20	−
2	IX 17	+	±30	?
Dn-1	VIII 3	+	48	+
A	VIII 13	−	79	+
Ps-/SA-B	IX 24	+	25	+
B. diversus				
DD-D	X 28	−	150	+
F	IX 28	+	16	?
5	VIII 21	−	±80	?
6	〃 14	+	130~140	?
***8**	X 27	+		+
12	X 3	?	?	+
13	IX 5	+	±200	+
DT-1	IX 8	dead	121	+
2	IX 27	+	51	?
B. ignitus				
Ig-A	IX 6	+	31	+
1	Early IX	−	±90	+
4	Late VIII	−	±130	+
6	VII 21	+	60	+
7	VI 23	+	77	−
	*VIII 12			−
9	VII 28	+	28	−
	*IX 19		40	+
B. hypocrita				
HH-1	VIII 29	+	40	+
2	VII 9	+	31	−
	*IX 20	−	18	+
HS-1	VII 15	−	96	+
B. arddens				
AA-6	Early VI	+	70	?
7	VI 15	−	30	+
	*VII 15			+
8	VI 16	−	85	+
	*VII 20		0	+
11	VI 6	+		+
	*VIII 9			+
AS-1	VI 25	+	25~30	+

AA-11, males laid after queens by the foundress is evident. In the course of W-M or Q, mixed batches frequently appear. It is noteworthy that Q-W batches appeared in **HH-2** and **HS-1**. Röseler (1974) found an elaborate mechanism of caste

after being reared in observation box, **=queen born batches alone)

Production of		No. mixed batches ($X=W$ or M)	Cocoons produced		% Q/total cocoons
Q	Laying workers		Total	Q	
−	−		63	0	0.0
+	?	4 *WQ*	203	46	22.6
+	?	4 *WQ*	134	31	23.1
−	+?	?	334	0	0.0
+	?	?	159	55	34.6
+	?	?	311	102	32.8
+	?	?	438	?	
−	?		±450	0	0.0
−	?		274	0	0.0
−	−		338	0	0.0
+	?	4 *WQ*, 7 *QM*?	489	41	8.4
−	+		860	0	0.0
+	+		835	14	1.7
+	?	1 *QX*	239	42	17.6
+	?		187	?	
+	?		±800	±250	±30
+	?		±1,300	±400	±30
+	?		364	52	14.3
−	−		174		
−	+?		245	0	0.0
−	−		67		
−	+		575	0	0.0
−	+?		340	0	0.0
−	−		106		
+	+	5 *QW*, 2 *QM*	366	23	6.3
+	+	1 *WM*	433	36	8.3
+	?		250	#	
+	?				
+	+		634	171	27.0
+	+				
+			717	269	37.5
+	−	6 *QM*	101		
+	+		238	101	42.4
			(198	101	51.0)**
+	?		208	10	4.8

determination in *B. terrestris*, which is consubgeneric with *B. hypocrita*. If the same mechanism is common to both species, mixed batches offer an interesting problem to be solved.

Worker ovaries were examined in **DT-1** and **HS-1**. Relation between head width and ovarian development behaved oppositely between two nests (Table 17). Ovarially developed workers were on the average larger in **DT-1** but smaller in **HS-1**. According to Cumber (1949) larger workers tend to develop ovaries in *B.* (*Melanobombus*) *lapidarius* but *vice versa* in other species. It is unknown whether above result reflects such specific difference, or more likely, different colony conditions, e.g. time since the appearance of laying workers.

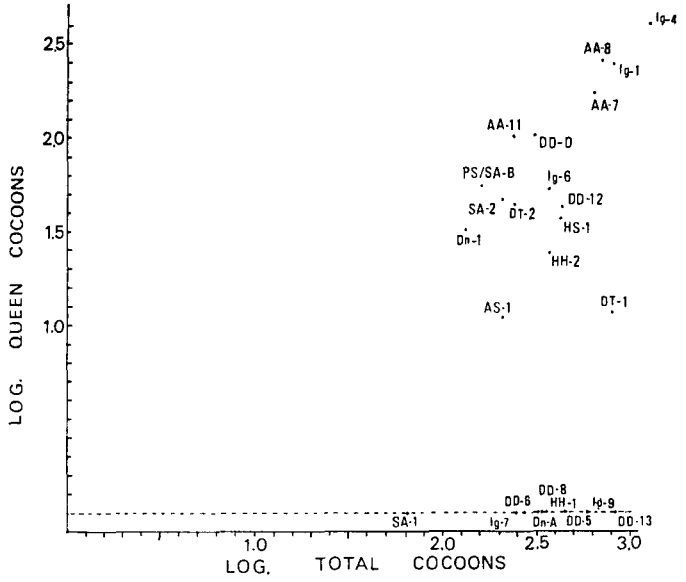

Fig. 21. Relation of queen cocoons to total cocoons in some nests attained to the climax stage.

14. Species and subgeneric specificities

Finally some probable species or subgeneric specificities are summarized by recombining comments given in preceding sections.

Thoracobombus: The features common to the studied forms of this subgenus are: 1) Preference for surface nest sites. 2) Absence of wax nest envelope. 3) Queen built egg cells relatively flat, not primed with pollen and built isolately between niches of cocoons with post-spinning immatures. 4) Presence of feeding pockets probably for sexual brood, too. 5) Colony size relatively small, the number of total cocoons rarely exceeding 200. 6) Batch arrangement basically rosette like. 8) Queen-worker size difference small.

Many if not all of these features would be common to other consubgeneric species, particularly to *B. veteranus* and allied species. Within the available

Table 17. Relation between head width and ovarian development in workers of two nests (Newly emerged *WW* excluded. Ovaries I=rudimentary, II=formation of some oocytes, IIII=fully developed)

Head width (mm)	DT-1			HS-1		
	I	II	III	I	II	III
2.2~2.3	1					
2.4~2.5	1					
2.6~2.7	3	2				
2.8~2.9	8	5				1
3.0~3.1	3	14	3			3
3.2~3.3	2	11	3			
3.4~3.5	4	8	10		1	2
3.6~3.7	2	11	7	1	1	6
3.8~3.9	5	3	6	2	1	11
4.0~4.1	2	4	1	1		5
4.2~4.3				11	6	7
4.4~4.5				14	4	3
4.6~4.7				4	3	
4.8~4.9				1	1	
% ratio	26.1	48.7	25.2	38.2	19.1	42.7

data, no specific difference among three forms studied is yet noticed.

Diversobombus: This subgenus is endemic to E. and S.E. Asia. No species other than *B. diversus* has been studied bionomically. The features common to studied nests and some related particularities are: 1) Predominantly underground nesting. 2) Mild temperament even in large nests. 3) Wax envelope facultatively present. 4) Queen built egg cells relatively tall, mainly built isolately on tops of cocoons with spinning and post-spinning immatures. 5) Presence of feeding pockets for sexual brood, too. 6) Colony size relatively large, not rarely exceeding 500 cocoons. 7) Batches relatively easily distinguished, and each batch probably large on the average. 8) Batch arrangement somewhat irregular. 9) Queen-worker size difference large. 10) Vulnerable to attack by *Mutila*.

The occurrence of closed feeding pockets (**DT-1**) and optional presence of egg cells primed with pollen (**DT-2**) should be studied in further nests.

Bombus s. str.: Bionomic features seemingly common to *B. ignitus* and *B. hypocrita* are: 1) Strong preference for underground nest sites. 2) Temperament more or less aggressive in large nests. 3) Wax envelope often present. 4) Queen built egg cells tall, not primed with pollen, built often contiguously at niches or tops of cocoons with post-spinning but not spinning immatures. 5) Feeding pockets absent. 6) Spinning cocoons easily broken and separated from batches. 7) Colony size relatively large, not rarely exceeding 500 cocoons. 8) Batch arrangement loose and irregular. 9) Queen-worker size difference large. 10) Resistant to attack by *Mutila*. 11) Frequent nectar stealing (observed both in

B. h. sapporoensis, Sakagami 1951 b and *B. ignitus*, Miyamoto 1961, Katayama unpubl.).

Items 1, 2, 3, 5, 6, 7, 8, 9 and 11 have been recorded in some consubgeneric species (Sakagami 1976, p. 435), together with presence of elongate pollen pots in the center of nest (**HS-1**). Other aspects interesting in comparative point of view are irregular orientation of worker born eggs, though also found in *B. d. diversus* (E. K. unpubl.). Except for difference in altitudinal distribution, no clear bionomic difference between *B. hypocrita* and *B. ignitus* was confirmed.

Pyrobombus: *B. ardens* can be characterized by 1) Colony cycle and phenology unusually short. 2) High plasticity in nest site preference, though nidification on exposed ground surface not confirmed. 3) Temperament mild even in large nests. 4) Wax envelope occasionally present. 5) Queen built egg cells relatively tall, usually primed with pollen, usually built in contiguity on tops or at niches of cocoons with post-spinning immatures. 6) Colony size medium with 200～300 cocoons. 7) Batches very difficult to separate and the whole nest mass compact. 8) Queen-worker size difference relatively large. 9) Vulnerable to attack by *Mutila*.

Among *Pyrobombus* *B. ardens* seems bionomically similar to *B. pratorum* in Europe by features 1, 2 and regular pollen priming. Contiguous building of egg cells is also remarkable. *Pyrobombus* is the largest subgenus in bumblebees and possibly involves several different modes of life (Hobbs 1967, Plowright and Jay 1968). Participation of new born queens in colony maintenance tasks and oviposition requires further studies.

Summary

Nests of some Japanese bumblebees were described and some characters were comparatively discussed. The forms involved are *Bombus* (*Thoracobombus*) *schrencki albidopleuralis*, *B.* (*Th.*) *pseudobacialensis*, *B.* (*Th.*) *deuteronymus deuteronymus*, *B.* (*Diversobombus*) *diversus diversus*, *B.* (*D.*) *d. tersatus*, *B.* (*Bombus*) *ignitus*, *B.* (*B.*) *hypocrita hypocrita*, *B.* (*B.*) *h. sapporoensis*, *B.* (*Pyrobombus*) *beaticola beaticola*, *B.* (*P.*) *ardens ardens* and *B.* (*P.*) *a. sakagamii*. Characters discussed are, habitat and nest site preferences, egg cells, feeding pockets, batch size, food storage, wax envelope, size difference among females, allometric trends in some metric characters, size- and age-linked worker polyergism, colony size and production of sexuals.

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