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Oviposition Behavior of a Brazilian Stingless Bee, *Plebeia (Friesella) schrottkyi*, with Some Remarks on the Behavioral Evolution in Stingless Bees[1)]

By

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(*With 9 Text-figures and 3 Tables*)

The present paper is an eighth report of our serial work on the oviposition behavior and related accounts of stingless bees (Sakagami, Sakagami et al. 1963～'71), dealing with observations on *Plebeia* (*Friesella*) *schrottkyi* (Friese), a tiny species of the size of a large Drosophila fly, distributed in Southern Brazil and forming an isolate monospecific group within *Plebeia* complex. First observations were made by S.F.S. and R.Z. in Rio Claro, SP, during March to April, 1963, and the result was briefly cited in Sakagami and Zucchi (1966). Later the study was supplemented by C.C. in Ribeirão Prêto from February, 1970 to July, 1971. Through these observations it has been clarified that this species involved two ethologically different types (Zucchi and Camilo 1971). Leaving detailed comparisons of them elsewhere, here the descriptions are confined to Type I observed since 1963. All colonies used were taken in or near Rio Claro, or were their descendants, all kept in heat conditioned observation hives (Sakagami 1966). The description and terminology follow those given in previous papers, especially Sakagami and Oniki (1963), Sakagami, Montenegro and Kerr (1965) and Sakagami and Zucchi (1967～'68).

1. Nest structure and behavior out of oviposition process

Following the sequence so far adopted in our serial work, some notes on nest structure and behavior out of oviposition process are preceded.

1) Behavior studies of the stingless bees, with special reference to the oviposition process. VIII.

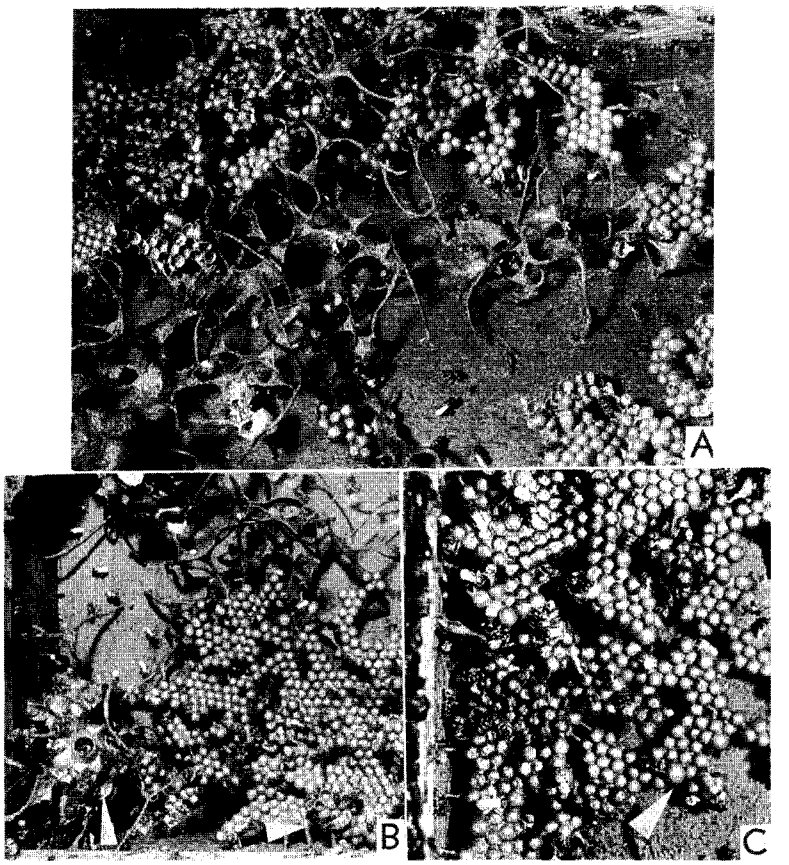


Fig. 1. Nest structure of *Friesella*. A. General view showing irregular comb arrangement and pillar system. B. Ditto, storage pots and the queen shown with arrows. C. Ditto, royal cell shown with arrow.

1.1. *Nest structure*: Concerning nest structure *Friesella* is intermediate between typical comb makers and typical cluster makers. Brood cells never form complete combs but also do not show an amorphous cluster arrangement as in *Hypotrigona* s. lat. (cf. Moure 1961) and *Frieseomelitta*. Cells are more or less juxtaposed but not neatly lie in the same plane. Each cell retains a spherical contour especially at top and bottom, resulting in a very uneven appearance of the "comb" (Fig. 1). Moreover this incomplete comb system does not always expand concentrically as in typical comb makers, often develops either spirally upward or unilaterally, forming an irregular band, which usually expands horizontally but can occasionally ascend or descend, and rarely even realizing a cluster arrangement. Many previous authors have referred to this irregular arrangement

(v. Ihering 1903, Mariano 1911, Moure, Nogueira-Neto and Kerr 1958, Wille 1969). Thus, *Friesella* is classified into incomplete comb makers which involve several systematically unrelated species such as *Trigona* (*Duckeola*) *ghilianii* Spinola (Kerr et al. 1967, Sakagami and Zucchi 1968) and *Meliponula bocandei* (Spinola) (Araujo 1955). Our observations show that "combs" of *Friesella* varies considerably among different colonies and in the same colony at different periods, fluctuating between relatively regular arrangement and quasi-cluster type. Worker brood cells are oval 2.2 mm wide and 3.5 mm long. No round cells recorded by Nogueira-Neto (1970) were observed.

Except two Australian species (Michener 1961) all typical cluster making species so far studied do not cover the brood area with involucrum. On the other hand, most if not all typical comb makers prepare involucrum. On this aspect *Friesella* is again intermediate. It does not build the genuine multi-sheeted involucrum, which completely separates the brood area from the other nest sections involving storage pots. Instead numerous thin and long pillars are constructed within the nest cavity, which, interconnecting one another, form an irregularly anastomosing network. Some parts of the network are further elaborated and small patches of irregular lamellae are produced here and there (Fig. 1, A). These lamellae can expand further, fuse together and sometimes incompletely cover the brood area. Further we occasionally observed, especially in outdoor colonies in winter, besides the lamellate pillar system mentioned, the construction of an incomplete single-sheeted involucrum, starting from the wall of the nest cavity or peripheral cells and expanding to the brood area.

Storage pots (Fig. 1, B) are round or oval, forming a mass, often with the walls common in adjacent pots and without differentiation of pollen and honey pots as in *Frieseomelitta*. Both brood cells and pots are pale brown, not whitish as in some typical cluster makers (*Leurotrigona*, *Celetrigona*). The entrance tube is short and narrow, constricted at the opening to allow the passage of up to 3~4 bees at the same time and at night closed with a delicate resinous network.

1.2. *Queen behavior and queen-worker coactions*: During inter-oviposition periods the queen does not continuously stay on combs. Her behavior is occasionally difficult to trace for she tends to stay in the shade of combs or pots, but she has no fixed resting places as in *Leurotrigona* and *Tetragonisca* (Sakagami et al. unpub.). Her walk is moderate, not so rapid and abrupt as in *Plebeia* s. str. (Sakagami et al. unpub.) but distinctly faster than in *Nannotrigona*, *Scaptotrigona* (Sakagami et al. unpub.) and especially *Duckeola* (Sakagami and Zucchi 1968). Either resting or at walk the antennae are constantly and fairly rapidly shaken and wings are rather continuously vibrated for a few seconds, intervened with momentaneous pauses.

The queen-worker coactions of *Friesella* represent the simplest type in stingless bees so far studied. Four basic patterns found in other groups (cf. Sakagami and Zucchi 1968) are confirmed but the royal court is virtually obsolete as to the

gravid queen. Even at prolonged resting of the queen, the number of attendants is very small, often absent and in the maximum not exceeding five. Workers met with the queen simply escape either immediately or after an instantaneous immobility or a mild advance toward the queen, without exhibiting any exaggerated or ritualized behavior patterns as seen in *Melipona, Scaptotrigona, Nannotrigona* and *Plebeia* (Sakagami et al., in part unpub.). Behavior of virgin queens will be described elsewhere.

Although no detailed observations were made, worker behavior is also simple. When interferred they do not show any defensive postures except for a brief exploration with antennae, followed by immediate retreat. There is, however, a trait which could be characteristic to *Friesella.* At least in the observation hive, it does not make large heaps of excrement as in other groups. We can see at most four to ten small patches of feces here and there on the floor of the hive. Such patches increase in number and size in cold and rainy periods, or in the weakened colonies, but do not grow into large masses as in other groups. The waste materials are carried away on the wing as in most other groups, not thrown from the entrance as in *Leurotrigona, Hypotrigona, Celetrigona* and *Lestrimelitta* (Zucchi et al. unpub.).

1.3. *Oviposition pattern*: Queen ovipositions of *Friesella* are typically batched, that is, several ovipositions succeed with brief intervals and the interval between these batched oviposition processes is relatively long. Henceforth the oviposition process relating to each cell is called *unit oviposition process* or UOP and batched ovipositions *integrated oviposition process*, IOP. The oviposition pattern is therefore similar to that of *Duckeola* (Sakagami and Zucchi 1968). It also resembles that of *Tetragona* (Sakagami and Zucchi 1967) and *Cephalotrigona* (Sakagami, Beig and Kyan 1964), but in these groups IOP occasionally disintegrates in the succession of several UOP separated by relatively long intervals. On the other hand, *Friesella* differs from *Melipona* (Sakagami et al.) in which, except some species, each UOP is mainly an isolate process, only rarely forming a small batch, or from *Scaptotrigona* (Sakagami and Zucchi 1963) in which each IOP forms a well organized entity by synchronous provisioning at several cells. The batched ovipositions are clearly demonstrated by the comparison of intervals between two successive UOP and two successive IOP:

Interval	Maximum	Average	Minimum
UOP (sec.)	853	196.98±133.92	32
IOP (min.)	678	236.92±142.99	41

From some observations lasting ten hours or more, the daily laying rate was calculated as 38.0 (one case), 42.5 (2), 50.0 (1), 50.5 (1), 52.5 (1), 57.5 (2), 62.5 (2) and 65.0 (1), in average 53.21±8.77, being higher than in *Melipona* species but not exceeding *Tetragona* (150~200, Sakagami and Zucchi 1967).

The number of cells oviposited in each IOP is 9.0±1.83 with the following

frequency distribution:

No. cells oviposited	1	4	5	6	7	8	9	10	11	12	13	15	16
No. cases observed	2	2	2	5	8	8	11	8	8	6	1	1	2
No. cases with unlaid cells		1		3	6	5	3	3	3	3			

Often some cells structurally ready to be oviposited, that is, provided with distinct collars (Fig. 2, stage V), remain unlaid in a given IOP, in part by the reason explained in **2. 1.** Such cells are usually oviposited in the next IOP but rarely remain till the next day or are destroyed. The number of cells remained in a given IOP, either structurally completed or not, increases in weak colonies. Among 31 IOP with unlaid cells, the frequency of cells unlaid was: one cell (22 cases), 2 (5), 3 (1), 4 (2), 5 (1), and the stage of cell (cf. Fig. 2) was: V (=completely collared, 22 cases), IV (8), III (7), II (3) and undetermined (7).

As in other groups so far studied, each cell is built by the summation of successive and "diffuse" activities of a number of young workers (Sakagami, Montenegro and Kerr 1965). Sakagami and Zucchi (1966) classified *Friesella* into the type with successive cell construction, in which cells are constructed at any time so that there are cells of various stages at a given time. After subsequent observations it seems better to regard *Friesella* as belonging to the semisynchronous type. As stated above no or only a few cells remain after an IOP (in average 1.55 $\pm$1.06) and most of them are provided with collars. As shown in Fig. 2, many if not all cells are rather synchronously started and the first cell is begun mostly within 10 min. (in average 6.25$\pm$2.75 min.) after the completion of the prior IOP. The time spent for the completion of one cell is variable among cells involved in a given IOP (Fig. 2), though the gradual development is a rule. Some cells are relatively early started but completed later (Fig. 2, A, cell 10, B, cell 5, C, cell 7) and some others *vice versa* (A, cells 7, 5, 6, B, 4, 2, 3). There is no correlation between the order of start of, and oviposition to each cell (Fig. 2). Some numerical data are given as follows:

Duration (min.)	Maximum	Average	Minimum	No. cases observed
Start to collared	240	130.36	60	59
Collared to oviposited	163	60.91	10	66
Start to oviposited	260	190.27	96	65

Fig. 3 presents a positive correlation between the number of cells in each IOP and the interval between two successive IOP. The fact that an IOP starts later if the preceding one involved many cells may be explained by the delayed increase of motivations both in queen and workers, in the queen in connection with delayed egg maturation and in workers correlated to the delayed increase of bees the crops of which are filled with larval food, which may secondarily affect the intensity of cell construction. The delayed start of an IOP when many cells are in preparation is more difficult to explain, though the distribution of labor among a more or less limited number of workers in many cells may in part be responsible. These correlations reveal that batched ovipositions are fairly stable in *Friesella*, giving a

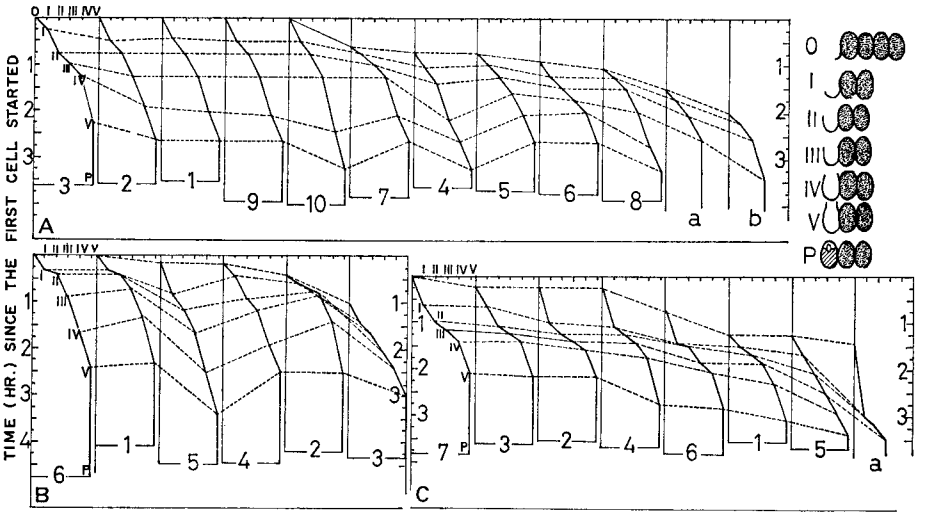


Fig. 2. Three continuous observations on the sequence of cell construction. A. 10 cells oviposited and two cells, a, b, left unfinished. B. 6 cells oviposited. C. 7 cells oviposited and one, a, left unfinished. Cell growth is divided into arbitrary stages 0~V shown at righthand top. Each cell is arranged from left to right in the descending order of the start of construction. Numeral given for each cell indicates the order of oviposition (P).

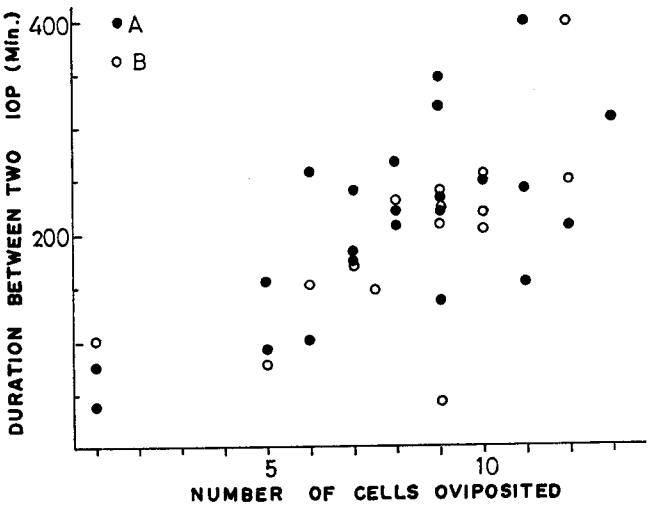


Fig. 3. Relation between number of cells oviposited in each IOP and duration between two IOP. A. Duration from the end of the prior IOP to the start of the process cited. B. Duration from the end of the process to the start of the next IOP.

regular rhythmicity to colony activities.

2. Oviposition process

As in other groups each UOP consists of several phases, Fixation (F), provisioning (P), queen oviposition (Q) and operculation (O), and an IOP is basically the repetition of this sequence for each cell, that is, IOP=n·UOP=n·(FPQO), where n is the number of cells oviposited. Corresponding to the degree of integration of each UOP in an IOP, some elementary phases, especially fixation and provisioning phases, receive certain modifications in temporal sequence. Such modifications are relatively inconspicuous in *Friesella* as subsequently described. Figs. 4 and 5 show the chronological sequence of some accurately observed IOP from the data obtained in 1963, where the queen behavior is taken as the focus of observations.

2.1. *Prefixation and fixation phases*: After the completion of several cells the queen visits combs from time to time, wanders around on them, stays by one cell or more for a while (=fixation to the cell) and leaves the comb away. The repetition of these visits and removals, *the prefixation phase*, is common to most stingless bee groups except *Nannotrigona* and, to some extent, *Geotrigona* (Sakagami and Zucchi unpub.). No precise observation was made on the temporal sequence of this phase. It can lasts from 30 min. to two hours. Thereafter the queen definitely stays by one cell until it is provisioned by workers. This is the fixation phase to the first oviposited cell or of the first UOP, and is called *the primary fixation* against *the secondary fixations*, that is, the fixation phase of the second and subsequent UOP. In *Tetragona* and *Duckeola* the primary fixation was in average longer than secondary ones, forming a prelude not only to the first UOP but to the whole IOP or n·(UOP). Such tendency is also traced in *Friesella* but the shortening of secondary fixations is less distinct than in two groups mentioned. The duration of the primary fixation is distributed in the data obtained in 1970～'71:

Duration (sec.)	～20	～40	～60	～80	～100	～120	～140	～160	～180	～200	～220	～240	～260	～280	～340
No. cases	3	33	47	31	21	12	7	14	4	4	5	3	3	4	3

The average is 151.6 sec. while that of secondary fixations 86.48 sec. (excluding wandering and temporary fixations to cells followed by wandering), shorter than the primary fixation but not so remarkably as in *Duckeola*. Table 1 shows the length of fixation in each UOP in four IOP illustrated in Figs. 4 and 5. The shortening of secondary fixations is traced in Nos. 1, 2, 3 but the sequence is not so conspicuous as in *Tetragona* and *Duckeola*. Fig. 6 gives the sequence of each UOP in five precisely observed IOP in 1970～'71. The temporal sequence is again irregular, probably indicating a weaker integration of UOP into IOP. Another difference from *Tetragona* and especially *Duckeola* is the frequent and often prolonged wandering on the comb appearing between two successive UOP with or without temporary fixations (cf. Fig. 6).

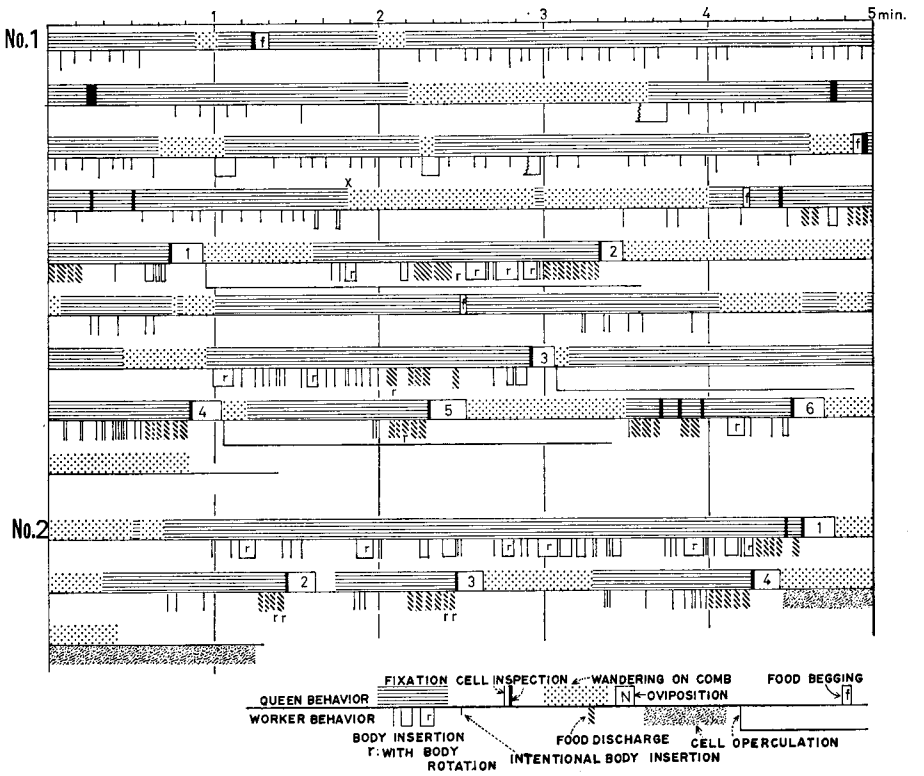


Fig. 4. Chronological sequence of two oviposition processes. No. 1. May 27 '63. Prefixation phase recorded. No. 2 May 26. Sequence relatively rapid. Intentional body insertions were recorded only in No. 1 (anterior half till mark "x"). Short-term behavior lasting less than one sec. is rounded to 1 sec. Correspondingly intervals between two immediately succeeded acts are not always exactly scaled.

Further the prolongation of secondary fixations to cells later oviposited is traced from the temporal sequence of IOP. The mean duration of successive fixations in some IOP with numerous cells was calculated as follows (sec.):
The same tendency was noticed in *Duckeola* and the explanation given there, the gradual decrease of workers participating in IOP, can also be applied to this case. Such decrease of provisioners is inferred also from the prolongation of provisioning phase as described in **2.2.** (cf. Fig. 5, Nos. 3, 4, Fig. 6, No. 9) and the failure of food discharges by workers in spite of persistent queen fixation (Fig. 5, Nos. 3, 4, final parts). The presence of cells structurally completed but remained unlaid described in **1.3.** is mostly noted in such situation.

Concerning the behavioral patterns involved, the oviposition process of *Friesella* is characterized by its simplicity. As in other groups so far studied, the

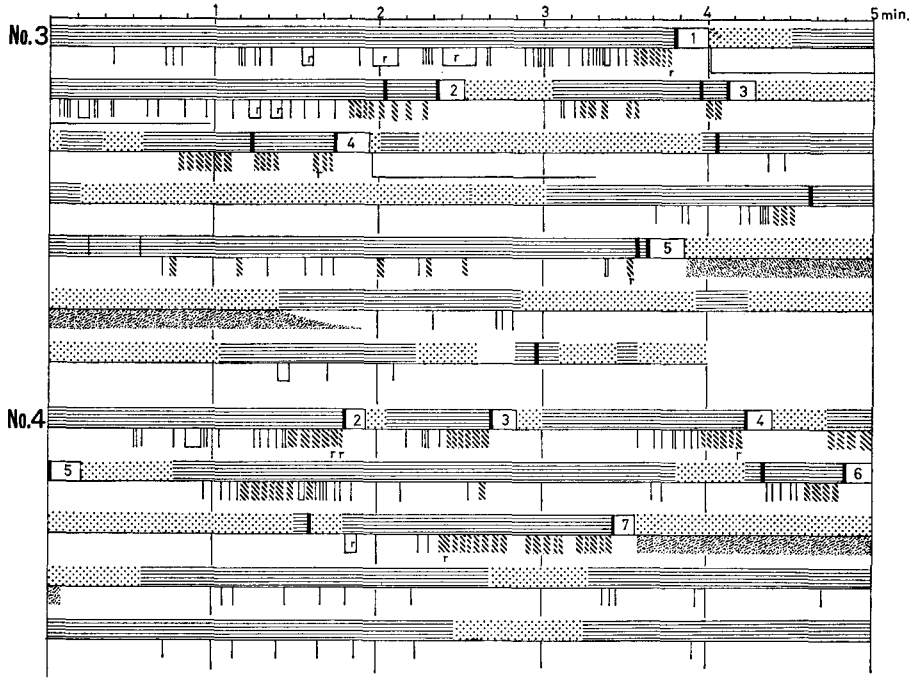


Fig. 5. Chronological sequence of two oviposition processes. No. 3 May 26 '63. Prolonged provisioning phase in the last cell and one cell remained unlaid. No. 4. May 28 '63. Observed after the first oviposition. One cell remained unlaid. Other explanations see in Fig. 4.

Table 1. Some numerical data on fixation phase in four IOP presented in Figs. 4 and 5. A. Duration since the end of the prior oviposition to the first food discharge to the cell concerned. B: Duration of fixation phase. C: Number of worker body insertions during fixation phase.

No. process	Order of oviposition																	
	1			2			3			4			5			6		
	A	(B)	C	A	(B)	C	A	(B)	C	A	(B)	C	A	(B)	C	A	(B)	C
1	—	(97)	5	77	(39)	4	514	(66)	17	751	(146)	75	6	(52)	2	59	(2)	1
2	—	(335)	34	90	(57)	3	37	(27)	4	82	(43)	9						
3	—	(333)	40	169	(139)	19	40	(10)	3	24	(4)	0	59	(25)	4	46	(33)	3
4		—		88	(88)	14	30	(22)	5	67	(58)	8	24	(4)	0	145	(35)	2

completed cells release concentration of several workers around them and their alternate body insertions (Fig. 7, E). Through repeated visits and temporary fixations by the queen to such cells, worker excitement gradually increases but

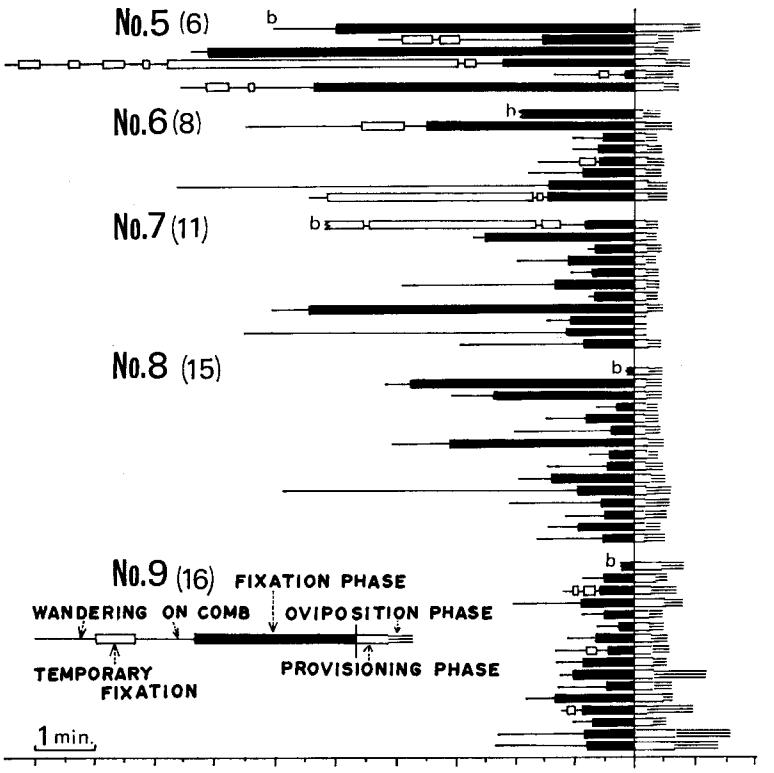


Fig. 6. Chronological sequence of each UOP in five IOP. Temporal sequence of each UOP is arranged from top to bottom, evened at the start of provisioning phase. "b". Beginning of observation. Numeral parenthetically given after each process number shows the number of cells oviposited.

never so exaggerated as in other groups studied. Therefore, prefixation and fixation phases cannot clearly be distinguished. Moreover, worker excitement is limited around the cell, never reaches a violent agitation spreading throughout the whole comb as is found, for instance, *Scaptotrigona* (Sakagami and Zucchi 1963), *Nannotrigona* and *Plebeia* (Sakagami et al. unpub.), probably in part due to the dispersed distribution of cells throughout incomplete combs (Fig. 8, E). There is another trait characteristic to *Fr. schrottkyi* Type I (not in Type II, Camilo unpub.) observed in the course of prefixation phase. In the absence of the queen, cell attendants which have alternately made body insertions cease any movements. All direct heads toward cells and take an akinetic posture. This "frozen rosette" (Fig. 7, A, center, B) is dissolved by the arrival of the queen but again appears after her removal until the fixation phase.

By the arrival of the queen, workers so far attended the cell escape from the



Fig. 7. Some behavioral patterns in oviposition process. A. Rosette formation at one cell (shown with arrow.). Queen fixing to the cell shown at lefthand (most cell attendants escaped). B. Rosette formation. Enlarged. C. Queen fixing to a cell. Worker attendants retreating from the cell. D. Queen begging food to a worker. Workers escaping from a collared cell. E. Concentration of workers to a completed cell with alternate body insertions. F. Queen beating a worker attending the cell. All worker attendants escaped from another cell nearby.

cell, frequently leaving the queen alone, who fixes patiently to such abandoned cell often for a considerable time. Or even if not escape from the cell, workers retreat downward along the cell wall (Fig. 7, A, lefthand, C). Only after a while

they advance to the cell opening but body insertions are strongly inhibited by the presence of the queen, mostly replaced by intentional ones, i.e., slight advance followed by immadiate retreat without actual insertion as mentioned in the first half of No. 1 with short vertical bars (Fig. 4). Consequently, real insertions are rather rare in the presence of the queen and increase usually (Figs. 4, 5, especially Nos. 2, 4) but not always soon before the first food discharge. The number of body insertions in fixation phase is distributed as follows with the average 12.10± 9.54.

No. insertions	0∼10	11∼20	21∼30	31∼40	41∼50
No. cases	79	43	12	7	1

During the fixation phase, there appears occasionally rather prolonged body insertions, mostly accompanied with body rotation. Many if not all of them are regarded as intentional food discharges without actual regurgitations.

As to the queen behavior during fixation phase, the following characteristics were observed: 1) No fixation to the cell with incomplete collar, as occasionally appearing in *Tetragona*, was observed. 2) By the arrival at the cell, the continuous wing vibration is replaced by rather intermittent beats, each of which is sometimes a simple stroke but usually a brief vibration. 3) The queen beats the worker inserting the body into the cell violently with antennae and fore-legs (Fig. 7, F). 4) This beating is often directed to the worker attempting to make insertion, often accompanied with a slight darting to the latter. The worker retreats or escapes from the comb, either soon or after patiently beaten for a while. No counter-darting by workers to the queen is observed nor any ritualized behavior. This queen behavior contributes in part to decrease real body insertions during fixation phase. 5) Cell inspection by the queen is very rare. She may inspect at the first visit or during prefixation phase, but does only rarely throughout fixation and provisioning phase until the inspection immediately before the oviposition as shown by the following frequency distrubution (fixation phase alone): 0 (60 cases), 1 (35), 2 (2), 3 (1), with the average 0.32+0.54 (cf. Figs. 4 and 5). 6) Queen inspection is very brief, seldom much exceeding one second, and simple, inserting only the lower half of the head, only rarely the whole head. 7) During prefixation or fixation phases, the queen occasionally begs food to the worker, resulting in a buccal contact which lasts 2∼3 sec. (Fig. 7, D), but actual food delivery by the worker was never confirmed. 8) The temporary fixations are occasionally long even if workers escaped from the cell. Among 31 observed cases, 11 were less than 10 sec., 14 less than 30 sec, two one minute and four 2∼4.5 min.

2.2. *Provisioning phase*: The provisioning phase starts by the beginning of the first food discharge and ends by the beginning of queen oviposition. The behavior pattern of food discharge resembles that in other groups. The body insertion is accompanied with a rapid metasomal contraction. As in *Tetragona* but more often the discharger rotates herself about 1/2 to 3/4 circumferences along

the cell margin (as shown in Figs. 4 and 5 with "r"). After discharge the worker rapidly escapes from the cell as in other groups but she usually returns to the cell and participates in the process as an attendant. The first discharge is usually followed by the second and subsequent ones. The duration of each discharge was measured as follows with the average of 1.87 sec. (SD=0.70): ≤2 sec. (185 cases), ≤3 sec. (178), ≤4 sec. (38), >4 sec. (11).

The temporal sequence of provisioning phase is divided into two types: 1) All discharges succeed rapidly so that the discharge subphase is relatively short. The postdischarge subphase is very short and no behavior appears during the phase. 2) Cases showing some deviations from the first type. The first type, which involves the majority of cases, is regarded as normal. Concerning these two types observations made in 1963 and 1970～'71 are somewhat different so that the results are separately described.

In 1970～'71 most cases belonged to the normal type. The abnormal cases involved one to three queen inspections during the phase, but the number of food discharges and duration of provisioning phase (average 12.41±4.61 sec.) did not vary much as follows:

Number of food discharges	Without queen inspection	With 1～3 queen inspections
3	26	6
4	80	13
5	16	3
Total	122	22

Duration of provisioning phase (sec.)	7	8	9	10	11	12	13	14	15	16	17	18	19	20	25	27
Cases observed																
With queen inspection	1	7	20	23	19	15	8	6	11	1	4	3		1	1	
Without queen inspection			1	1	1	1	2	3	3	2	1	4				2

The duration of postdischarge subphase was not measured in all cases but was quite short in general: 0 sec. (5 cases), 1 (9), 2 (1), 4 (1), 5 (1) (Queen inspection before oviposition not included).

On the other hand, a marked irregularity appeared in 1963. Among 21 cases illustrated in Figs. 4 and 5 only ten (No. 1, cells 4, 5; No. 2, cells 2, 3, 4; No. 3, cell 1; No. 4, cells 2, 3, 4, 5) are considered as normal. Even in these cases, the number of food discharges is higher than in 1970～'71 (4 discharges/4 cases, 5/1, 6/5) and the discharge subphase longer (9.5～20 sec., in average 15.4 sec. Postdischarge subphase not particularly longer, 0～1 sec., average 0.55 sec.). In two other cases (No. 2, cell 1; No. 3, cell 2), one queen inspection appeared during discharge subphase (Number of discharges 5 and 7, duration of discharge subphase 16 and 29 sec., of postdischarge subphase 1 and 3 sec.). Other nine cases were quite abnormal in sequence. The number of discharges varied 5～18, in average 9.9, and the duration of discharge subphase 26～249 sec. in average 88. 3 sec. The postdischarge subphase was long in No. 1–1 (31.5 sec.), No. 1–3 (26 sec.) and 1–6 (33 sec.), but short in others (0～3 sec.). In these cases the rapid succession of food discharges was interrupted, intervened with queen inspections (cf. Nos. 1–6, 3–3, 3–5) or worker body insertions (Nos. 1–2, 1–3, 3–5). In an extreme case (No. 4–6) the queen once abandoned the cell.

Certainly these abnormal cases indicate that the colony was observed under food

deficiency. In other species, prolonged postdischarge subphase is characteristic to the first cell oviposited in *Scaptotrigona* (Sakagami and Zucchi 1963) and appears facultatively in *Tetragona* and *Melipona* species (Sakagami et al.). In *Friesella* the prolongation of postdischarge subphase appeared frequently, often accompanied with irregular sequence. The rapid succession of food discharges is a rule in most groups and species so far studied, with a single exception of *Melipona compressipes manaosensis* Schwarz, probably due to abnormal colony condition (Sakagami and Oniki 1963). In *Duckeola* even at an apparent food deficiency the first discharge was always followed by rapid succession of subsequent ones. For the time being, it is uncertain whether the irregular sequence observed in *Friesella* represents a trait frequently appearing or reflects some special colony conditions.

Finally three additional observations are given as to the provisioning phase: 1) In *Friesella* laying workers appear in orphan colonies (Camilo unpub.) but no deposition of trophic eggs was observed in queen-right colonies, nevertheless worker ovaries can develop under such condition (Sakagami et al. 1963). 2) Provisioning for the royal cell was once observed in 1971. Reflecting the size larger than worker cells (4.1 mm wide and 6.6 mm long), eleven discharges were made in rapid succession, followed by two brief body insertions by workers before the inspection and oviposition by the queen. 3) In other groups a worker cell is filled with food about up to 2/3 of its capacity. In *Friesella* the cell is filled with food nearly up to the upper margin. *Nannotrigona* (Sakagami and Zucchi unpub.) exhibits a similar tendency but not so exaggeratedly as in *Friesella*.

2.3. *Oviposition and operculation phases*: As in other groups, the queen oviposition is invariably preceded by an instantaneous cell inspection, with the insertion of only the lower half of the head into the cell. The queen oviposition is relatively long (average 13.43±3.24 sec.) with the following frequency distribution: 6 sec. (1 case), 7 (3), 8 (6), 9 (13), 10 (58), 11 (63), 12 (61), 13 (68), 14 (53), 15 (47), 16 (35), 17 (22), 18 (19), 19 (7), 20 (10), 21 (4), 22 (1), 23 (5), 24 (3), 26 (1), 28 (1). During the oviposition (Fig. 8, B, D) the queen vibrates wings but makes no particular movement of legs. The egg stands erect or slightly inclined and is rather deeply inserted into the larval food (Fig. 8, C).

The cell operculation, started 1.85±1.03 sec. after the queen oviposition, is very characteristic. In all so far studied groups the operculation is begun by one worker who sits on the cell, inserts her metasomal tip in the cell and works by rotating the body on the cell (=rotation subphase). Only later she withdraws the metasomal tip and after a brief continuation of rotation or without such, works sitting at the side of the cell (=sidework subphase). In the latter subphase often other workers participate in the task to complete the cell lid. In *Friesella*, however, the operculation is made since the start by 5~6 workers, each of which stands at the side of the cell, directing the head to the cell orifice and works without rotation and consequently the differentiation of two subphases (Fig. 7, A, E,). The average duration of the operculation is 119.32±31.99 sec. with the following frequency distribution: 50~60 sec. (2 cases), ~80 (9), ~100 (49), ~120 (54), ~140 (31), ~160 (16), ~180 (17), ~200 (8), ~220 (1), ~240 (1). Some prolonged cases

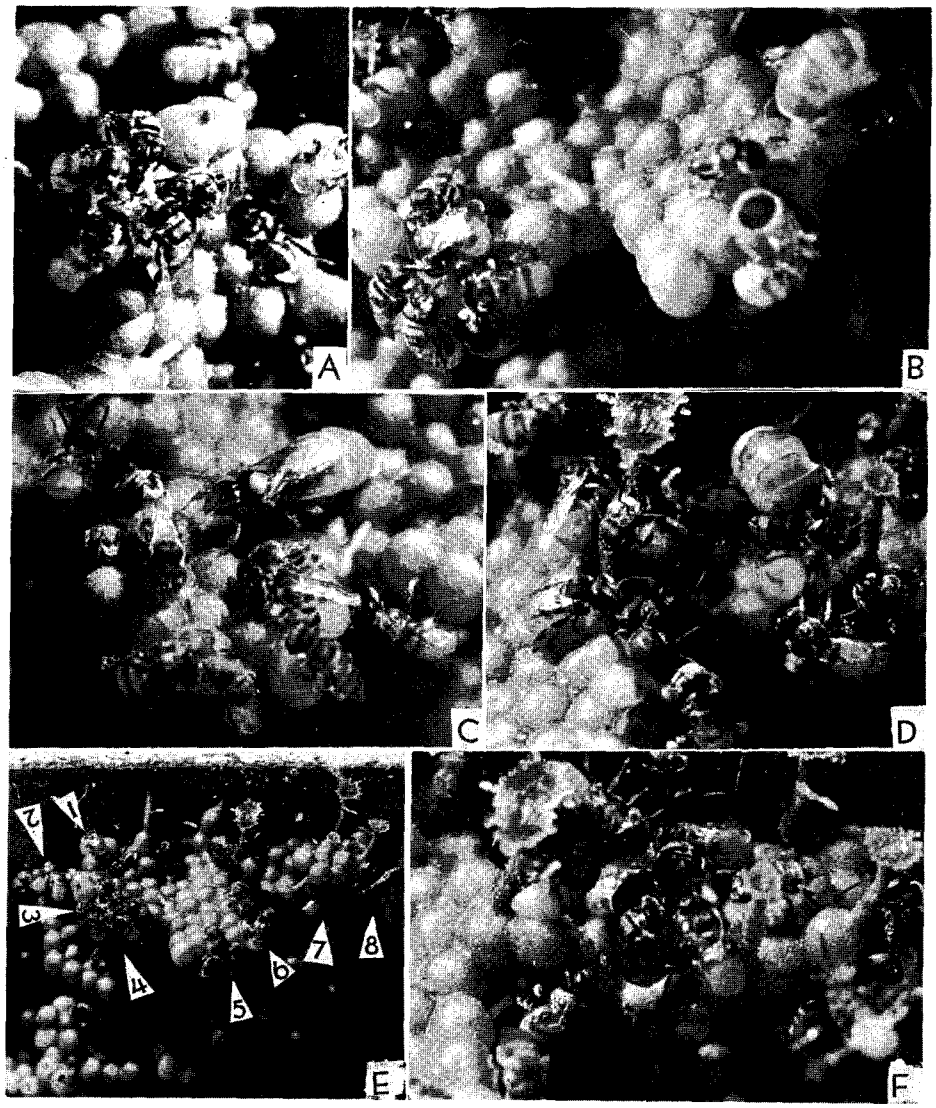


Fig. 8. Some behavioral patterns in oviposition process. A and F. Operculation of an oviposited cell by several workers. B. Queen oviposition (right). Another still unlaid cell (left) attended by workers. C. Escape of workers operculating a cell by approach of queen. An egg is visible in the cell. D. Queen oviposition. E. Cells at diverse phases. 1. Final stage of operculation. 2, 4, 5, 6, 7. Before provisioning, attended by workers with alternate body insertions. 3. In operculation. 8. Cell with queen fixation.

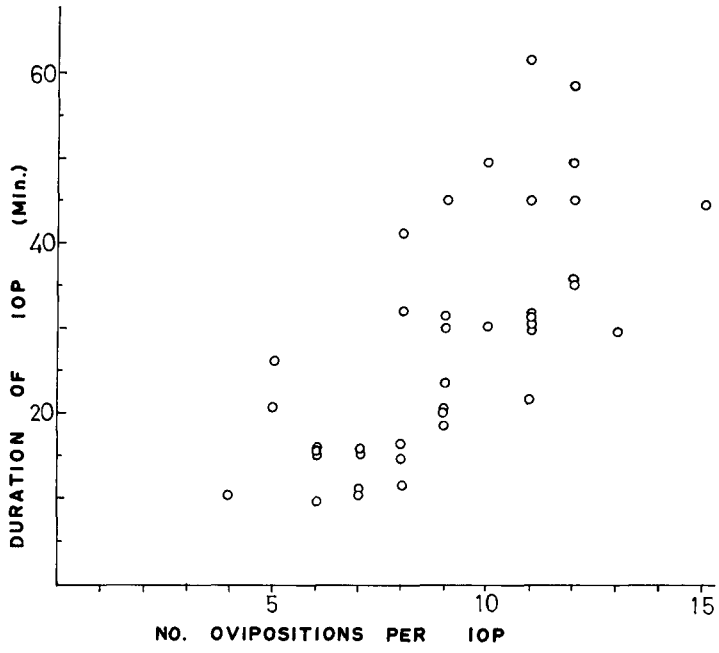


Fig. 9. Relation between duration of IOP and number of cells oviposited.

were caused in part by the approach of the queen which released the escape of workers (Fig. 7, C).

The time spent for an IOP (measured from the beginning of the primary fixation) was recorded as follows: 9 min. (1 case), 11, 13 (each 2), 15 (1), 17, 19 (each 2), 20, 21 (each 3), 22 (1), 23, 27, 29 (each 2), 30 (3), 32 (2), 33 (1), 34 (2), 36, 37, 42, 44 (each 1), 45 (2), 49, 57, 63 (each 1), in average 25.87 min. The duration lengthens in IOP including many cells (Fig. 9).

Discussions and remarks

Here the behavioral peculiarities of *Friesella* are summarized and some preliminary remarks on the behavioral evolution in stingless bees, with special reference to *Plebeia* complex, are added to.

1. *Peculiarities of* Friesella *in oviposition behavior*: The behavioral sequence in the oviposition process of *Plebeia* (*Friesella*) *schrottkyi* Type I shows the succession of several phases as in other stingless bees so far studied. Further there are several characteristics common to the other groups or species, which are: 1) Increased body insertions by workers in prefixation phase. 2) Rapid succession of food discharges by workers, though it did not occur in some presumably abnor-

mal cases. 3) Escape of workers from the cell after food discharge. The relation of workers to the queen out of oviposition process also shows some patterns common to other groups: 1) Gradual formation of royal court around the resting queen. 2) Repetition of rapid advances followed by retreats by attendants in front of the queen. Excluding these items, an ethological description of the species observed is given below, with special reference to queen-worker coactions and oviposition process, in comparison with the groups on which behavior observations were already published: *Scaptotrigona* (*S*), *Melipona* (*M*), *Cephalotrigona* (*C*), *Tetragona* (*T*) and *Duckeola* (*D*), using the following symbols: Similar to (=), different from (≠), similar but more conspicuous (others≤), similar but less conspicuous (≤others), more conspicuous (others<), less conspicuous (<others).

1) Cells arranged in incomplete horizontal combs (=*D*, ≠*SMCT*). 2) Involucrum absent (=*D*, ≠*SMCT*), except occasional formation of incomplete ones. 3) No differentiation of pollen and honey pots (=*DSMCT*). 4) Royal cells larger than worker ones (≠*M*, =*ST* and probably *CD*). 5) Waste materials carried away on the wing (=*DSMCT*). Queen vibrating wings (=*DT*), not beating (≠*SMC*), though not too continuously (≠*D*). 6) Queen walking with moderate speed (=*MT*), not too slowly (≠*SD*). 7) Queen not resting with geonegative posture (≠*D*, =*SMCT*). 8) Royal court very inconspicuous (≠*SMCTD*). 9) Exaggerated queen worker coactions absent (≠*SM*, =*CTD*). 10) Cell building not started by accumulating a large amount of cerumen on side wall of another cell (≠*D*, =*SMCT*). 11) Cell building semisynchronous (≠*SMCT*, =*D*). 12) Oviposition process always batched (≠*MCT*, =*SD*), but food discharges to each cell strictly successive (≠*S*, =*D*). 13) Shortening of secondary fixations inconspicuous (*M*<, <*TD*, ⋘*S*). 14) Prefixation and fixation phases not clearly separable (≠*SMCT*, =*D*). 15) Queen not fixing to cell without complete collar (≠*T*, =*SMCD*). 16) Primary fixation relatively persistent, not intervened by frequent wandering (≤*D*, <*ST*, =*M*). 17) Queen cell inspection in fixation and provisioning phase rare (<*SM*), never rhythmically repeated (≠*CTD*). 18) Queen beating violently workers inserting body into cell (≤*M*, *SCTD*<), occasionally even darting to them (≠*SMCTD*), 19) At initial part of fixation phase workers markedly intimidated by the presence of queen, causing scarcity of body insertions (*MCTD*≤), never showing exaggerated response (≠*S*), 20). In later part of prefixation phase workers attending cell forming "frozen rosette" in the absence of queen (≠*SMCTD*). 21) During provisioning phase queen normally not wandering to other cells (≠*S*), nor making peculiar retreat from cell (≠*M*, =*CTD*). 23) Worker oviposition during oviposition process absent (=*D*, ≠*SMCT*). 23) Queen oviposition relatively long (⋘*M*, *SD*<, *TC*⋘) made without peculiar twitching of legs (≠*D*, =*SMCT*). 24) Cell operculation starting soon after queen oviposition (=*SCD*, ≠*T*, = or ≠*M*). 25) Operculation made since beginning by several workers sitting at sides of cell without rotation and subphase differentiation (≠*SMCTD*).

Some of these characters might vary according to colony conditions, but many if not all are seemingly species- or group-specific. The most outstanding feature

of *Friesella* is the last mentioned item, cell operculation, which is unique in all stingless bees so far studied. Item 14, 17～20 are also characteristic but shared with some other groups. Item 20 is not shared with any other groups but also vestigeal in *F. schrottkyi* Type II (Camilo unpub.). Leaving detailed discussions of these characters for the future, some preliminary remarks on the behavioral evolution in stingless bees, with special reference to *Plebeia* complex, are given below.

2. *Nest pattern diversity in* Plebeia *complex*: According to Moure (1951, 1961), whose supraspecific system is being tentatively adopted in the present serial work, the genus *Plebeia* involves four Neotropical subgenera, *Plebeia*, *Schwarziana*, *Friesella* and *Mourella*. He also regards the Australian *Austroplebeia* as its subgenus and some African groups such as *Plebeina*, *Plebeiella*, and *Meliplebeia* as close relatives. In the lumping system by Wille (1963) all above mentioned groups and the African *Apotrigona* are included in the subgenus *Plebeia* of the genus *Trigona* (Wille 1962, '63, '64). Further he regards this *Plebeia* complex and *Nogueirapis* as the most primitive groups among the stingless bees, assuming the appearance of the earliest stingless bees during Eocene as small, *Plebeia*-like bees. If this opinion is correct, the behavior characters in *Plebeia* complex is important to trace the evolution of stingless bees.

First we shall refer to the diversity of nest pattern found in *Plebeia* complex, which was recently put in order by Wille (1969) as summarized in Table 2. Adopting the idea developed by Michener (1961), Wille assumed the evolutionary course of A→B→C→D→E. According to him and Michener, if the cluster arrangement found in diverse stingless bee groups is primitive, combs must have arisen independently in some groups. "It seems unlikely that the habit of organization of cells to form almost identical combs would arise repeatedly and independently, while it seems that the disorganization of comb to produce the cluster arrangement might more easily occur independently in various phyletic lines." (Michener 1961). Therefore the specialized cluster type given in Table 2 is regarded by them as a secondary derivation from the comb type as an adaptation to the small and irregular nest sites, accompanied with the reduction of involucrum. On the other hand, the cluster type of *P. australis* and *P. cincta* with spherical and not necessarily upward directing cells is regarded as representing the primitive conditions.

A few comments are given with respect to the opinions cited above: 1) Secondary derivation of cluster arrangement by disorganization of combs is certainly conceivable. But it may not necessarily exclude the possibility of independent evolution of comb system within stingless bees. Wasps and bees apparently developed their comb systems independently. In each of these groups, parallel evolution of comb system is assumed within halictine bees (Sakagami and Michener 1962) and probably within stenogasterine wasps (cf. Yoshikawa, Ohgushi and Sakagami 1969). It is likely that the comb system, the arrangement of many cells of the same size concentrating in the same plane, must have evolved repeated-

Table 2. Various nest patterns found in *Plebeia* complex. Prepared from Wille (1969)

Symbol	A	B	C	D	E
Type	Primitive cluster	Intermediate cluster	Horizontal comb	Irregular horizontal comb	Specialized cluster
Nest cavity	Relatively large	Relatively large	Relatively large	Relatively large	Small
Cell arrangement	Irregular clusters	Irregular concentric layers	Horizontal layers	Irregular horizontal layers	Irregular clusters
Cell shape	Spherical	Spherical	Vertically elongated	Vertically elongated	Vertically elongated
Direction of cell openings	Mainly but not necessarily upward	Upward to laterally	Upward	Upward	Upward
Involucrum	Single-sheeted	Singlesheeted	Usually multi-sheeted, sometimes only patchy or absent	Absent	Absent
Species involved	*australis*	*cincta*	Most *Plebeia*	*schrottkyi*	*minima*, *tica*
Moure's subgenus	*Austroplebeia*	*Austroplebeia*	*Plebeia*	*Friesella*	*Plebeia*

ly as a consequence of labor economy. 2) Spherical cells found in *Austroplebeia* could be the primitive type as asserted by Wille. But if these represent the type ancestral of stingless bee cells, it must be concluded that the earlier stingless bees already developed a cell type highly specialized as a bee group, because brood cells of most bees are of the elongated type irrespective of the materials and techniques adopted. 3) Another minor addition is that cells tend to become less elongated even in specialized cluster type than in comb type. The ratio of length /width (in mm) in some species cited in Table 2 is as follows; A. *P. australis* 3.5/3.5 (1.00) (Michener 1961). B. *P. cincta* 2.7/2.7 (1.00). (Michener 1961). C. *P. droryana* 4.17/2.16 (1.93). D. *P. schrottkyi* 3.53/2.21 (1.59). E. *P. tica* 4/2.5 (1.60) (Wille 1969). Thus, irrespective of primitive or specialized conditions, cells seem to shorten in cluster type not organized in combs. Similar short cells are widespread in *Hypotrigona* s. lat. though not in *Frieseomelitta* with clustered cells, probably correlated with the elongate body. Finally the occasional appearance of involucrum in *P. schrottyki* described in **1.1.** complements Table 2.

After these comments, the evolutionary course assumed by Wille, which involves the derivation of type D represented by *P. schrottkyi* from Type C of most *Plebeia* s. str. (Henceforth *Plebeia* is used in the strict sense) is still possible. Now let us compare the oviposition behavior of *Friesella* and *Plebeia*.

3. *Comparison of oviposition behavior between* Friesella *and* Plebeia: *Plebeia* is one of the most prosperous Neotropical stingless bee groups including numerous species. We observed only four, *P. droryana* (Friese), *P. emerina* (Friese), *P. remota* (Holmberg) and *P. jullianii* Moure, all belonging to the horizontal comb makers. The results of observations are still not well prepared and will be published in a later paper. But in spite of obvious variations according to colony

Table 3. Synoptic comparison of oviposition behavior between *Friesella* and *Plebeia* s. str.

Character	*Friesella*	*Plebeia*
1. Walk of queen	Moderate and relatively constant	Often quite erratic, accompanied with abrupt darting
2. Worker response to queen	No particular response except those common to other stingless bees	Highly exaggerated, with frequent darting and/or peculair "hypnotic turning"
3. Cell building	Semisynchronous	Synchronous
4. Differentiation of prefixation and fixation phase	Obscure	Distinct, the latter characterized by high excitation of both castes
5. Fixation type	Prolonged fixation to each cell	Virtually no fixation to each cell. Queen running over comb throughout IOP
6. Worker excitation	Weaker, confined to each cell	Violent, spreading over comb
7. Provisioning	Each cell successively provisioned	All cells nearly synchronously provisioned
8. Queen inspection before oviposition	Always present	Only in a few cells first oviposited, later absent
9. Queen oviposition	Mostly longer than 10 sec.	Never exceeding five sec.
10. Cell operculation	Since beginning made by several workers sitting at cell sides. Solitary rotation never made	By a single worker first rotating on cells, later sitting at cell side, with occasional participation of other workers
11. Worker oviposition in queenright colonies	Never observed	Absent during oviposition process. Present in prefixation phase on or at sides of combs, when encountered with queen. Queen oophagy not necessarily appearing, even if after inspection of worker born egg

conditions and species, there are several decidedly constant features common to all species observed, which are compared in Table 3 with *Friesella*. In both groups ovipositions are clearly batched. Otherwise there are many remarkable differences. First we deal with the peculiarities of *Plebeia*.

Among the features given in the table, items 3～8 reveal the highly organized IOP in this group, in which each UOP is nearly absorbed inside the whole IOP. Consequently, the total duration of IOP is relatively short. A few examples of the duration since the first food discharge to a cell to the final queen oviposition are given: *P. emerina* 6 min. (involving 50 cells), 7 min. (61), 13 min (64); *P. droryana* 8 min. (27), *P. remota* 5 min. (16), 4 min. (11), 6 min. (22). Apparently the whole IOP proceeds very rapidly under high excitation, which shows the highest degree of organization among nearly all stingless bee groups so far observed by us. Therefore *Plebeia* is highly specialized in oviposition behavior even though morphologically still undifferentiated as thought by Wille. Three interpretations can be held to resolve this discrepancy: 1) The highly organized oviposition behavior appeared already at an inicial step of stingless bee evolution, which has been kept by *Plebeia* until the present but disorganized in other groups, with or without secondary modifications. 2) The ancestral stingless bees did not develop such advanced organization, which was achieved by *Plebeia* after its segregation from other groups, though it retained primitive morphological features. 3) *Plebeia* is variable with respect to oviposition behavior, involving other unspecialized patterns still not discovered.

The last interpretation must always be kept in mind. We must continue to increase further comparative observations, particularly on the species building cluster type nests or those showing borderline morphological features (for instance, *Plebeia intermedia* Wille, being intermediate between *Plebeia* and *Schwarziana*, Wille 1960). But the basic resemblance of behavior pattern in four species observed by us suggests that the highly organized pattern is widespread in the group, at least among comb making species which occupy the majority. Between two other alternatives we would like to prefer, for the time being, the second interpretation as a more plausible working hypothesis. The disintegration of organized structure and its further reorganization may have repeatedly appeared in the course of many evolutionary processes. To explain a given phenomenon, however, it ought to be postulated only when the undeniable evidence is available or when no other explanations are possible. The adoption of the second interpretation implies that *Plebeia* cannot simply be regarded as a primitive group, even if it retains many primitive morphological features, because, once established, ethological characters are "in general" not necessarily inferior to morphological ones in evaluating the phyletic position of a given taxon (Sakagami and Yoshikawa 1968).

Then, how could we interpret the relation between *Plebeia* and *Friesella*? The items 3～8 clearly show in themselves that oviposition behavior of *Friesella* is less organized. Here again we can put three interpretations, that is, *Friesella* represents, 1) type ancestral to *Plebeia*, 2) type secondarily disorganized from that

shown by recent *Plebeia* and, 3) type ramified from the main trunk before the appearance of the organized pattern exhibited by recent *Plebeia*.

The first interpretation is fairly reasonable as far as items 3～8 are compared, but decidedly rejected by item 10. Among more than 20 groups of stingless bees observed by us, only *Friesella* performs the cell operculation without solitary rotation. The use of metasomal rotation for cell operculation or related work is widespread among bees, for instance, in halictine bees (*Lasioglossum*, Batra 1964), xylocopine bees (*Ceratina*, Tano 1964) and, though no comprehensive bibliographical survey was made, in several wasps. Moreover, the operculation behavior in *Eulaema nigrita* Lepeletier (Euglossini, Zucchi, Sakagami and Camargo 1969) is nearly identical with that found in most stingless bees, including the differentiation of rotation and sidework subphases. On the other hand, the operculation since the start with mandibles is seen in orphan colonies of some species (*Cephalotrigona*, *Partamona*, Sakagami et al. 1964) but is never so efficiently made with continuous participation of several workers as done by *Friesella*. This trait is considered as a specialization probably developed in relation to the large amount of food put in each cell (cf. **2.2.**). By this single character *Friesella* cannot be placed at the bottom of the dendrogram of not only *Plebeia* complex but also the whole stingless bees.

Nextly let us examine the relative validity of the second and third interpretations. Both are possible as far as the items 3～8 are concerned. The disorganization of integrated behavior pattern may be facilitated in irregular combs such as built by *Friesella*, where the spread of excitation may be less smooth than on typical combs. But we prefer the latter interpretation by two reasons. One is the same to that adopted in discussion about *Plebeia*. The disorganization of an integrated behavior process is surely possible but we would like to avoid its application as far as possible, especially when dealing with such highly organized pattern as seen in *Plebeia*. The second, still inconclusive reason is derived from item 11, the absence of trophic eggs produced by workers in front of the queen. A previous study (Sakagami et al. 1963) confirmed ovarially developed workers do appear in queenright collonies of both *Plebeia* and *Friesella*. But the production of trophic eggs in front of the queen in *Plebeia* is assumed as the step more advanced than in *Friesella*, judging from the specialization of stingless bees in this trait (cf. below).

Consequently we assumes that *Friesella* separated from *Plebeia* before the latter developed a highly organized oviposition behavior. By this conclusion we agree with Moure (1961) in treating *Friesella* as an isolate side branch of *Plebeia*, irrespective of they are regarded as subgenera or mere species groups. Further we cannot admit the derivation of *Friesella* from recent *Plebeia* with combed nests. But this does not necessarily invalidate the hypothesis held by Wille. Because the derivation of *Friesella* from a *Plebeia* like ancestor, which already possessed combed nests but still not the highly organized oviposition behavior, is possible.

The assumptions given above are still not free from criticisms by the lack of

more comparative data, both within *Plebeia* and *Plebeia* complex. One group belonging to the complex, *Apotrigona*, was recently studied by Darchan (1969, a, b, *P. nebulata komiensis* Cockerell). Its oviposition behavior seems to be similar to that of *Plebeia*, though more precise description is required. Another group placed in *Plebeia* complex by Moure, *Schwarziana* with a single species, *P. quadripunctata* (Lepeletier), exhibits the oviposition behavior completely different from both *Friesella* and *Plebeia* (Sakagami and Zucchi unpub.).

4. *Some additional remarks on behavioral evolution in stingless bees*: Using this occasion, we want to correct our previous hypothesis held as to the evolution of worker oviposition in stingless bees (Sakagami and Zucchi 1969). Based upon the widespread appearance of the inhibition of ovarian development in workers by the queen in social insects, we regarded the stingless bees which did not develop worker ovaries under queenright condition as the primitive type (=honeybee type) and those exhibiting ovarian development and production of trophic eggs, being prevalent in most Neotropical groups, as a more specialized type (=stingless bee type). We believe this assumption is still valid. But the group cited as representing the first type, *Duckeola* and *Frieseomelitta*, were seemingly not appropriately selected. Because recently Terada (unpub.) confirmed in *Trigona* (*Frieseomelitta*) *varia* (Lepeletier) the absence of worker ovarian development even under orphan conditions. Although further critical studies are required, this suggests a specialized condition diametrically opposing to other stingless bees, because it might imply a final phase of caste differentiation, where workers ultimately lost the capacity to develop ovaries even in the absence of the queen. Thus, the species representing the honeybee type in stingless bees must be chosen from other groups. Probably *Hypotrigona* (*Leurotrigona*) *mülleri* (Friese) is an appropriate example, in which worker ovaries are atrophied in queenright condition but develop in orphan colonies, resulting in the production of laying workers (Terada unpub., Sakagami and Zucchi unpub.), as just seen in the honeybee. It is difficult to assume the relative position of *Friesella* with respect to this evolutional trend. The queen inhibition must have been incomplete in the inicial steps as in bumblebees and halictine bees (Sakagami and Hayashida 1968). The presence of ovarially developed workers in queenright colonies in *Friesella* could be regarded as showing this step, being more primitive than *Leurotrigona*, or might represent a step more advanced in the direction of the stingless bee type. Further quantitative analysis of ovarian states in workers now undertaken by one of us (C.C.) may clarify the situation, but our inference given in the preceding section, considering *Plebeia* as more advanced than *Friesella*, is not affected by it.

The behavior study of *Plebeia* complex is important when considering its affinity with *Melipona*, which was already pointed out by Schwarz (1932) and admitted both by Moure (1951, 1961) and Wille (1963). No contemporary meliponologists may deny that *Melipona* is a highly specialized group. Notwithstanding the oviposition behavior of this genus is the least organized among all

stingless bees in the sense that each UOP is quite independent one another (cf. Sakagami, Montenegro and Kerr 1965, Camilo 1972). Our interpretation of *Friesella* could also be applied to here. Namely, *Melipona* separated from the main stock resembling *Plebeia*. Thereafter it developed a series of specializations but retained an unorganized oviposition pattern. In this case, however, the secondary simplification is also likely in connection with the low oviposition rate characteristic to the genus.

An interesting but still inconclusive behavioral affinity between *Plebeia* and *Melipona* is added to. In the course of behavior studies with numerous stingless bee species, two of us (S.F.S. and R.Z.) are gradually being convinced of an assumption that the core of the complicated oviposition process in this group is a conflict in workers between fear to the queen and defense of the cell against her. This hypothesis is still premature and will be developed elsewhere, but various responses of workers to the queen suggest its reliability. On the other hand, the queen seldom exhibits any aggressive behavior in most groups so far studied. The exception is *Plebeia* in which the queen often drives away workers, especially during the oviposition process. This tendency is observed, far less conspicuously, in *Friesella*, too. If the ever increasing differentiation between castes is regarded as an index of evolutionary trend in social insects, such dominating behavior in queen is assumed as representing a primitive condition and its disappearance as an advanced state. In most species of *Melipona* observed by us, however, the queen often touches the worker crouching in her front with a highly ritualized manner (Sakagami, Montenegro and Kerr 1965, Camilo 1972). Probably this signifies that the original dominating disposition of the queen disappeared in other groups while it was retained in *Melipona* after receiving a marked transformation.

The stingless bees are ethologically highly diversified groups. The interpretations of their behavior is achieved only through careful comparisons of various groups and species. Some hypotheses presented above may and must be tested through such tedious comparative observations. Finally it must be mentioned that numerous papers devoted to the construction of a meliponid dendrogram by Kerr and his collaborators (cf. Kerr 1969) were intentionally not cited in the present paper, because this work involves many characters, principally non exomorphological ones, and their precise evaluation and incorporation into the discussion must be left for the future.

Summary

The oviposition behavior of *Plebeia* (*Friesella*) *schrottkyi* (Friese), forming an isolated group within the large *Plebeia* complex, was observed by using several colonies taken in Rio Claro, S.P., Brazil. This species makes incomplete horizontal combs. Brood cells are built semisynchronously and ovipositions are typically batched to form an integrated process (IOP), in which each unit process (UOP) proceeds successively. The most conspicuous trait in this species is the absence

of rotation subphase in cell operculation, which is unique among all stingless bee groups so far studied. Other behavioral characteristics to be mentioned are: Formation of a "frozen rosette" by worker attendants around the cell not visited by the queen in prefixation phase, rarity of cell inspections by the queen, violent touching by the queen of workers in fixation phase and relatively long queen oviposition. Some evolutionary considerations on stingless bee behavior were added to.

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