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Oviposition Behavior of the Stingless Bees, XVII. *Plebeia* (*Plebeia*) *droryana* and an Ethological Comparison with Other Meliponine Taxa (Hymenoptera, Apidae)

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Abstract The cell provisioning and oviposition process (POP) of *Plebeia* (*Plebeia*) *droryana* is mainly characterized by: 1 – always batched ovipositions; 2 – synchronously constructed and provisioned brood cells; 3 – interactions between castes remarkable by the queen's frequent and abrupt motions allied to her overt aggressiveness, eliciting complex and diversified worker behaviors; 4 – worker-born trophic eggs laid anywhere on the comb long before food provisioning, and eaten either by the queen or by other workers. Although the POP of most stingless bees always shows some agitation involving both castes mainly at food provisioning into cells, the agitation seen in *P. droryana* reaches the highest level, which is, only comparable to that in *Nannotrigona* and *Mourella.*

Key words: Stingless bees; *Plebeia*; oviposition behavior; social evolution.

Introduction

As emphasized in our serial work, the behaviors involved in the food provisioning and oviposition process (POP) of stingless bees are unique among social insects as to their complexity. The comparative analysis of POP is important to recognize phylogenetic relationships among various supraspecific taxa, because the POP is remarkably taxon-specific. In addition, such studies may help to understand the genesis and evolution of the social organization because the POP proceeds along with diverse and complex queen-worker interactions.

This 17th serial report deals with the POP of *Plebeia* (*Plebeia*) *droryana*, based on observations of six colonies conducted in the chronological order by S. F.S., R.Z., DE SANCTIS, S. M. and P.M.D. The first draft was prepared by P.M. D. and R.Z., and then it was checked and improved by S.F.S. and S.Y.

Material and Methods

Plebeia (*Plebeia*) *droryana* (FRIESE) nests in several kinds of cavities such as tree hollows, man-made constructs and less frequently earthen banks. It is a typical comb builder presenting the whole brood area covered with multi-layered involucrum. The colonies of *P. droryana* were collected and studied in the State of São Paulo, S. Brazil. The initial qualitative observations were developed in Rio Claro on colony 1 during Oct.–Nov. 1962 by S.F.S. and R.Z., the summary of which appeared in SAKAGAMI & ZUCCHI (1966). Then, additional data were gathered in Ribeirão Preto on colony 2 (Feb.–Mar. 1971 by DE SANCTIS & R.Z.), colony 3 (Dec. 1988 by R.Z.), colony 4 (Oct. 1989 by S.M. & R.Z.), colony 5 (several occasions during 1990–1992 by S.M. & R.Z.), and colony 6 (Jun.–Oct. 1991 & Mar. 1994 by P.M.D., and Apr. 1994 by S.M.).

Taxa cited for comparisons are informally mentioned in the text with generic or subgeneric names. Those not cited in the references were taken from our unpublished data. Only asterisked papers of our serial work are cited in the references, all the others can be found in SAKAGAMI *et al.* (1993)*. Worker-born oocytes are referred to as eggs or trophic eggs. Behavioral terms mainly follow SAKAGAMI & ZUCCHI (1974)* and SAKAGAMI *et al.* (1993)*. In winter, heated observation hives (SAKAGAMI, 1966) were generally used. Otherwise, most colonies were kept in simple wooden boxes with glass lids. In all cases hives were settled in the laboratory and connected with outdoors by a transparent plastic tube. Since the basic behavior patterns and sequences little varied among observed colonies, the results are jointly shown without citing each colony unless some particularities occurred.

As in the other serial studies, observations were focused on clarifying behavioral sequences in the course of POP. Descriptions were gradually improved by repeated observations of unmarked bees, later often with the use of video recording.

Temporal structure of POP

This part, important to apprehend the POP structure exactly but somewhat complicated by its very nature, has been so repeatedly explained that only a brief essence is given here. The daily colony rhythm of a queenright colony involves the succession of three periods (quiescent, transient and oviposition periods), i.e., $n(\bar{Q}+\bar{T}+\bar{O})$. Such a sequence is clear in S_yB_e taxa (e.g. *Nannotrigona*, cf. Diagnosis D16, D17) but less in other taxa with many cells ready for use at any time (S_cB_f taxa, e.g. *Mourella*). Next, $\bar{O}$ consists of $\bar{P}+\bar{A}+\bar{O}'$ (patrolling, arousal and oviposition stages). In D_c type taxa with cells provisioned successively (cf. D18), the oviposition stage of each cell ($\bar{u}_i$) involves four phases (predischarge, discharge, oviposition and operculation or $\bar{r}_i$, $\bar{d}_i$, $\bar{o}_i$, $\bar{s}_i$), i.e., $n\bar{u}_i = n(\bar{r}_i+\bar{d}_i+\bar{o}_i+\bar{s}_i)$. In D_y type taxa with cells provisioned synchronously (D18), however, $\bar{r}_i$ is not differentiated in each $\bar{u}_i$, appearing only in $\bar{u}_1$ while omitted in the subsequent $\bar{u}_n$. Details are given in Sakagami & Zucchi (1974, Fig. 12)*, and its citations in Sakagami (1982, Fig. 19) and Sakagami *et al.*, (1993, Fig. 1)*.

Results

The qualitative state of each behavioral character in *Plebeia* is itemized in: "Ethological features common to other taxa" (items C1–C21) and "Ethological diagnosis" (items D1–D42) at the end of "Results". These items are frequently cited below in the text as C*n* or D*n*. The other parts of "Results" deal with aspects necessary to understand the diagnosis. Most quantitative data are lumped together under "Quantitative data".

Behaviors not involved in POP

Despite the occasional appearance of dwarf gynes, all the observed colonies were headed by normal queens, who were larger than workers, especially in head, mesosomal and metasomal widths. Out of $\bar{O}$, the queen has hardly been seen on the comb except for brief visits. Unlike queens of *Leurotrigona*, she has no definite resting spot (D7). Her locomotion is characterized by abruptness (D9). She sometimes rests quietly, but suddenly starts running about with remarkable speed and irregular body shaking. Here and there she makes brief stops in front of cells under construction, examines these calmly with wings closed and resumes her running. Her wings are sometimes closed together but, while resting or walking, are usually spread out and continuously flapped. Each stroke is longer and weaker than in *Nannotrigona*, involving irregular substrokes which occasionally change into vibration, especially during walking (D11). The retinue behaviors, besides those features common to other taxa (C14–C20), involve some peculiar traits also (Table 1). The asynchronous wing movements that characterize *Scaptotrigona* workers are not present. Occasionally some workers pulled a leg or wing of the queen with their mandibles (colony 1). This probably represents an abnormal situation, because in other instances such an event relates to aggressions leading to queen supersedure.

Table 1. Behavioral patterns involved in queen-worker interactions of *Plebeia droryana*: A. actions elicited by the approaching queen when cells are still under construction, B. same as A, in relation to a particular worker who inserts her forebody in a cell, and C. interactions during retinue behavior.

Behavioral interactions (all worker acts except asterisked)	A ($n=90$)	B ($n=90$)	C ($n=81$)
Simple backing	39	—	—
Rapid escaping	28	—	3
Incomplete hypnotic turning	17	7	45
Rapid non-specified contact	7	—	17
Worker oviposition	3	—	5
Darting	2	—	1
Crouching	2	—	18
Buccal contact*	1	—	3
Full hypnotic turning	1	1	7
Staying in the cell	—	73	—
Retreating from the cell	—	16	—
Mutual head pushing*	—	3	1

Except for *n* (number of observed cases), other numerals are expressed in %. Other explanations are in the text.

* queen-worker interacts.

The most remarkable behavioral interaction is certainly hypnotic turning (ht) (Fig. 1). Although it appears occasionally in *Nannotrigona* and *Trigonisca*, it is much more frequent and generally fully expressed in *Plebeia.* This interaction involves the resting or wandering queen and a worker in her front. If a worker suddenly encounters the queen, she usually escapes rapidly, but sometimes she lowers her head and raises her metasoma by stretching her mid and hind legs. Then, as if hypnotized, she turns around very slowly, until she is perpendicular or often parallel to the queen. At this step the worker lies just or nearly below the queen's head. Then, the worker draws the legs which are turned to the queen and stretches those on the opposite side. As a result, the worker's body is inclined towards the queen. Usually, the queen leaves after touching the worker with antennae or mandibles, but sometimes the akinetic worker is strongly seized and gnawed by the queen. At calm encounters, behaviors do not much alter, but the queen's hurried running invariably evokes rapid escape of workers nearby. Even if the preliminary stage of hypnotic turning has been started, the queen's agitation leads to the omission of some behavioral components (=incomplete ht, Table 1). Occasionally a worker stays in front of the queen, taking the posture which is similar to ht, as if disturbing her proceeding. This "hypnotic barricading" is seen more frequently and exaggeratedly in the allied taxon *Schwarziana.* While the hypnotic turn appears even in callows, the worker's darting to the queen is rare. When it occurs, it is simple and invariably

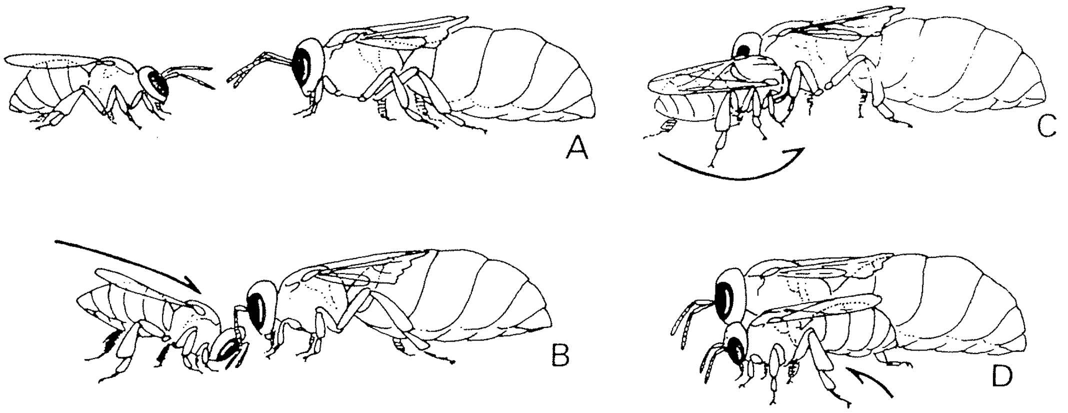

Fig. 1. Hypnotic turning of the worker to the queen in *Plebeia droryana*. A: Encounter; B: Darting at the queen who lowers the head; C: Slightly inclining the body and very slowly turning toward the queen. D. Sitting beside the queen and slowly edging herself towards the queen with the body inclined (cited from SAKAGAMI, 1975*).

directed to the queen's head, and never so elaborated as in *Nannotrigona*. Some dartings can elicit strong buccal contacts, almost always started by the queen probably as a modified food soliciting. Its seemingly aggressive nature (possibly homologous to the behavior taken by the dominant females of *Polistes* wasps) is suggested by the manner that the queen sometimes holds down and strokes the worker with drumming antennae and forelegs. Nevertheless, the real food exchange is rare. Food transfer between workers is frequent and elicited by far less elaborated interactions. Possibly such a queen-worker contact is a vestige of effective food transfers, which currently no longer plays such a role. Other kinds of queen-worker interactions are shown in Table 1, and in DRUMOND & BEGO (1994).

Waste materials are usually piled in the nest. Some workers take small pieces from such a spot with their mandibles and carry them away on the wing (D6).

Cell construction, oviposition rhythms and trophic eggs

In most so far ethologically described taxa, the construction of each brood cell starts anytime and thus cells at various growth stages coexist. Although not so precisely as in *Nannotrigona* (SAKAGAMI *et al*., 1993)*, the cell construction in *P. droryana* is synchronous (Fig. 2). Moreover, all collared cells are invariably oviposited within the same POP, and only exceptionally a few ones remain untreated. These anomalous cases are usually caused by food shortage (SAKAGAMI *et al*., 1993)*, and POP in such cells is postponed until the next batch. Because of the synchronous construction and short duration of Q and T (Fig. 2), the time necessary to complete one cell nearly equals the duration of construction of all cells composing the batch. Other information is given in "Quantitative

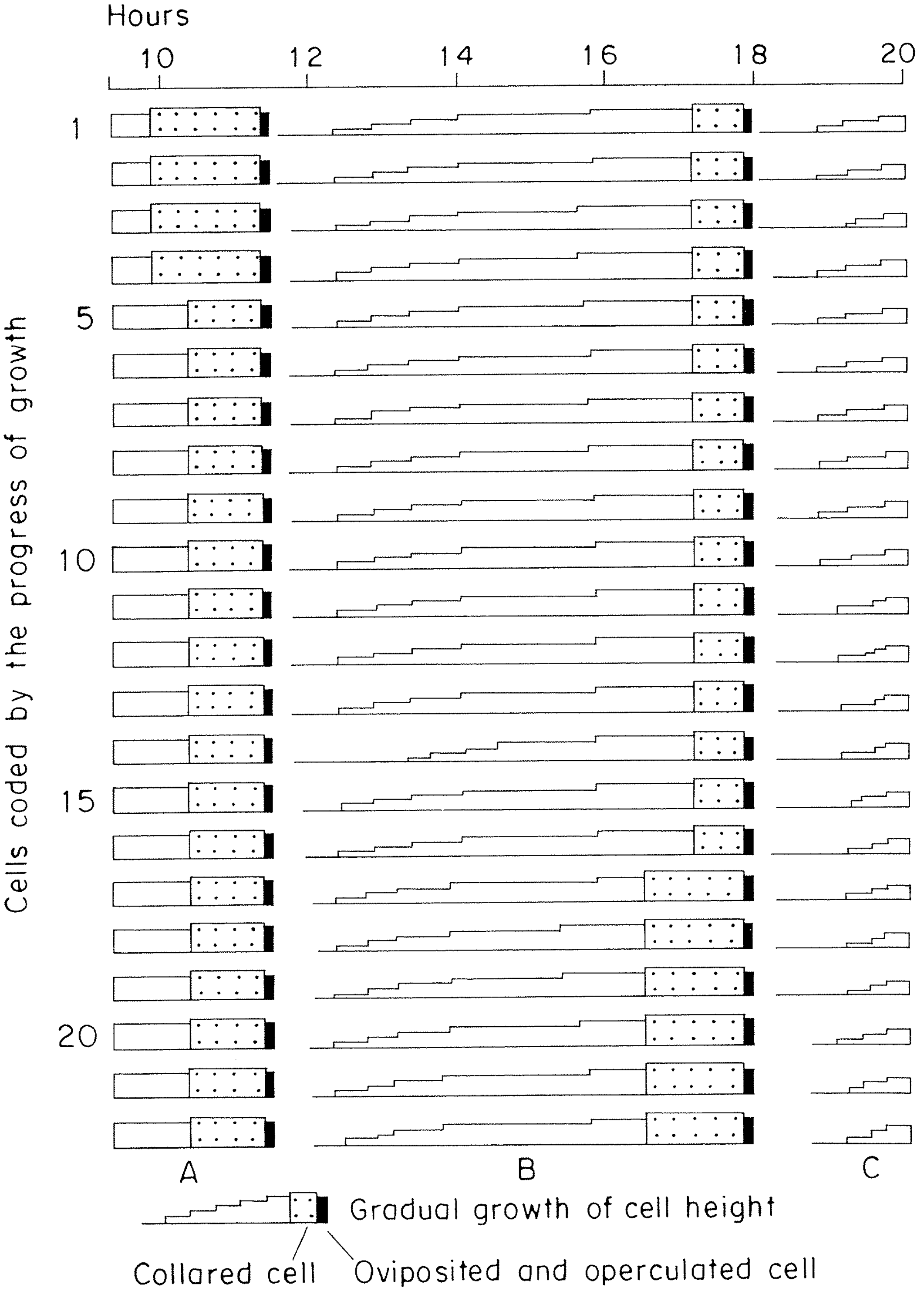

Fig. 2. Cell construction and oviposition sequences of 3 successive POPs, A, B and C, recorded in colony 6 of *Plebeia droryana*. In all cases batch size=22 cells. Cell growth was fully recorded in batch B, while in batches A and C only the final and early parts of the POP were depicted, respectively (April 1994).

data".

As mentioned in *Nannotrigona*, each new cell is started in contact with a cell oviposited in the previous batch. Thus, batch size tends to be similar in some of the subsequent POP, provided food and thermal conditions are adequate. Although such correlation was not particularly analysed in *Plebeia*, Fig. 2 shows the same batch size (22 cells) in three sequential POP. This favors our hypothesis on the influence of stereotyped behaviors as possibly eliciting the synchronized POP sequence (Sakagami *et al.*, 1993)*, although the final solution still needs further comparative studies.

One of the remarkable traits in stingless bees is certainly the presence of laying workers in queenright colonies. In most analyzed taxa, worker-born eggs are laid after d̄ (food discharge phase) and are soon eaten by the queen. But in *Plebeia droryana* workers oviposit either on the advancing front of the comb or at its margin long before d̄. The worker's laying is apparently stimulated by the queen who behaves as if asking for food (see Behaviors not involved in POP). Indeed, the queen taps the prospective laying worker violently with her antennae and forelegs, and holds the worker down by persistent gnawings which can be turned into buccal contacts. Sometimes, while trying to escape from the queen the worker bends her metasoma downwards, and oviposits with her wings spread slightly. Under such situation the detection of trophic eggs in *P. droryana* is quite difficult, e.g., only 10 such eggs were found in colonies 2 and 3. Motivated by such scanty results, they were intensively looked for in colony 6. By recording worker ovipositions between successive POPs throughout seven sequential daily periods (32 h in total) 36 worker ovipositions were observed (3% during Q, T; 94% in the course of cell construction and 3% after appearance of collared cells). Besides, as observed by Terada (unpubl.) there were two types of trophic eggs: oval-yellowish and thin-transparent. The presence of such egg differentiation, although more exaggerated in size, has been previously recorded only in *Scaptotrigona* (Akahira *et al.*, 1970; Beig, 1972). From the prevalent fate of such eggs in *Scaptotrigona*, the larger ones were considered nutritive eggs while the thin eggs were assumed producing males. The present result suggests that this interpretation is correct only partly, because the both types of *P. droryana* worker-born eggs are laid only on the comb surface, generally well apart from cells, and thus even the thin eggs can not develop. Observations on the fate of 98 worker eggs (including 36 cases mentioned above) showed that they were entirely (31%) or partly (17%) eaten by the queen. The workers ate the remaining eggs (52%) and all the remains left by the queen. In addition, two interesting facts were recorded: 1 – the occurrence of an yellowish drop between the mandibles of the laying bee, which is regurgitated and absorbed in the course of the laying, 2 – the deposition on the comb of metasomal fluid instead of an egg. Such a droplet is immediately taken by a nearby worker.

The diverse behaviors involved in queen-worker interactions are summarized in Table 1.

Behaviors before food provisioning

During P and A, behavior sequence of the workers proceeds as in other taxa. As usual in most studied stingless bees, the final part of cell construction, which is characterized by the appearance of collared cells, involves rapid body insertions in cells by workers. The substitution of one inserting worker by another (worker alternation) becomes gradually more rapid and agitated. This involves the shift of cell construction motivation to intentional food discharges. Meanwhile, the queen continues to stay on the comb front, running around its margin and examining some cells briefly (Fig. 3). Her locomotion is so rapid that workers in her course either escape away or are virtually driven out, resulting in the rarity of court formation, and also in the virtual absence of any other behaviors during the most agitated phase of POP.

Any worker performing cell insertions (Table 1, B) usually escapes when touched by the queen, but sometimes she persists, and inclines her body towards the queen often not withdrawing her metasoma from the cell. Obviously this

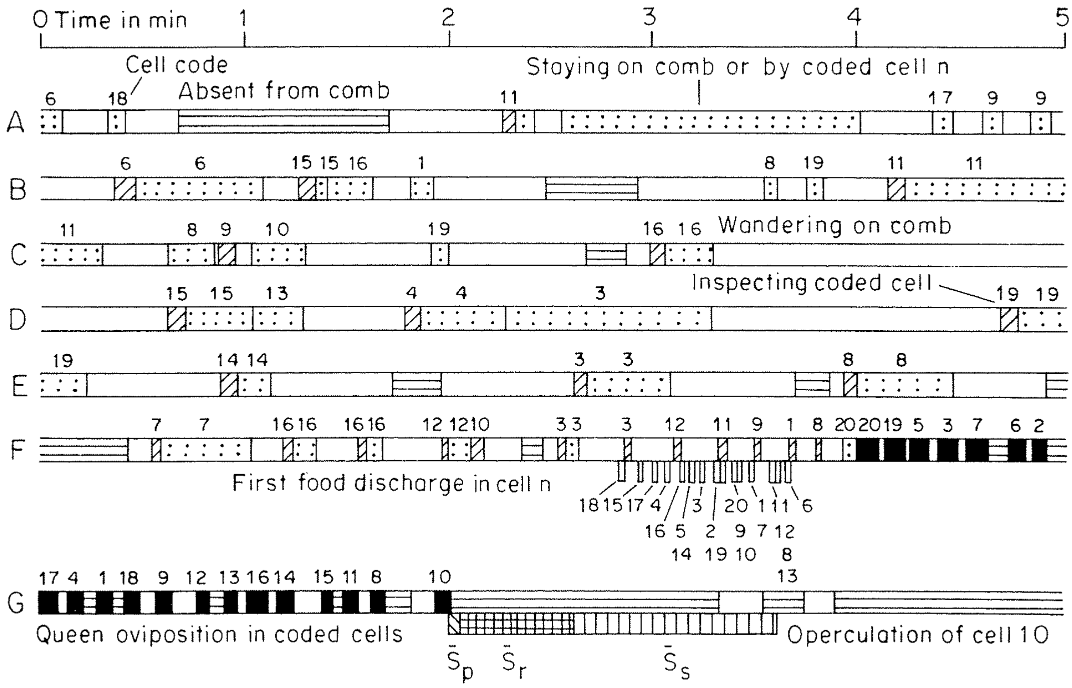

Fig. 3. Behavior sequences in the POP of colony 6. Sequences A–E show queen behavior only; Sequences F and G show the queen's (above) and workers' (below) behaviors: Start of cell provisioning in each coded cell (F, below), and operculation of the last oviposited cell (G, below) are detailed. Numerals = cell codes where specific behaviors were displayed. (Batch size = 20 cells, April 1994).

indicates a mild expression of hypnotic turning. The persistence of such a worker can evoke a kind of "tour de force" between the worker's firm metasomal insertion into the cell and the queen's try of removing her. Sometimes continuous pulling out by the queen is useless due to the worker's particular position. But usually the queen succeeds in her persistent pulling and violent gnawing and tapping all over the worker's exposed body parts. As soon as the worker gets off the queen inspects the cell.

The duration of $\bar{A}$ is much shorter than that of $\bar{P}$, and in its course the agitation gradually increases. This is first noticed in the behavior of cell insertion by workers. It becomes shorter while worker alternation is virtually immediate. Besides, many workers and the queen perform frenzy running all over the comb. Even under such agitation the queen occasionally leaves the comb though she soon returns there.

Provisioning, queen oviposition and operculation

Behaviors of *P. droryana* during the most agitated phases of the POP could be precisely traced by video recording. As in *Nannotrigona* the cell first receiving food is not necessarily the last one visited by the queen (Fig. 3). Actually, the opposite cases often occur, and once, the first provisioned cell had not been visited by the queen before. But, despite such similar tendencies, the behavior traits of *P. droryana* queen differs from those of *Nannotrigona* because her locomotion pattern is higher and rapidly covers the area bearing collared cells almost entirely. Conversely, the *Nannotrigona* queen tends to sequentially concentrate her activities into localized spots of the comb, although she also does it agitatedly.

As in other so far studied taxa, the discharge of the first food droplet increases agitation even more. Within seconds all collared cells receive provisions almost synchronously. Food discharge in each cell is similar to that in other observed species. The first discharge is soon followed by a second and subsequent ones, and each worker withdraws from the cell after discharging. Other details are given in "Quantitative data". The behavior sequence in the postdischarge subphase ($\bar{d}_p$) is similar to that in *Nannotrigona.* Generally a worker attends the cell ($\bar{a}$), often encircled by others. Such an attendant constantly shakes her head and inspects the cell. The mandibles are opened, but the glossa is never extended so that she certainly will not add secretion into the cell. The same attendant can monopolize the cell throughout the subphase or can be substituted by another. After some cells have been provisioned, the queen starts ovipositing. She decisively directs herself to the cell, and the eventual worker attendant gives the way. Before ovipositing the queen invariably inspects the cell, often combined with a brief food intake mainly before her first oviposition. Queen oviposition is brief and simple. Except for metasomal contractions and movements of antennae and forelegs no other motions appear. Even their wings are kept closed. As in other studied taxa, provisioned neighbor cells tend to be oviposited successively, but without definite spatial order (Fig. 3).

The operculation of each cell usually starts soon after the queen's oviposition (=preoperculation subphase $\bar{s}_p$ is rare or short, even if present). The separation between rotation ($\bar{s}_r$) and sidework ($\bar{s}_s$) subphases is neat (=transient subphase $\bar{s}_t$ virtually absent) (Fig. 3).

Quantitative data

Each item is arranged in the order of variation range and, in the parentheses, arithmetic mean±sample standard deviation and sample size.

Time spent in 10 wing strokes by the queen at resting: 5.2–64.0 s (12.1±0.1; $n=206$) and while walking: 4.0–20.0 s (9.4±3.9 s; $n=197$). Duration of buccal contact: 1.0–7.0 s (3.8±1.5; $n=23$).

Time for the construction of all cells of a batch: 135.0–267.0 min (214.5±39.2; $n=14$). Time for Q+T: most cases, less than 10 min (Fig. 3). Interval between two successive POP's (measured from the end of the last operculation of a previous POP to the start of the first queen oviposition in the next one): 182.0–395.0 min (278.9±48.7; $n=16$). Batch size (=no. cells laid per POP): 5–40 cells (21.3±6.5; $n=70$). Approximate daily oviposition rate (colony 6): 79.4 cells per 24 h. Duration of P: 7.0–41.3 min (21.6±7.5; $n=36$). Duration of A: 72.0–410.0 s (235.5±72.6; $n=62$). Duration of provisioning in all cells of a batch: 12.0–27.0 s (18.9±3.6; $n=72$). Duration of provisioning in each cell: 15.0–25.0 s (19.3±3.0; $n=32$). Number of discharges necessary to provision a cell: 4–7 (5.1±0.7; $n=32$). Duration of each food discharge: 0.8–3.0 s (1.5±0.5; $n=140$). Number of worker body insertions during $\bar{d}$: 0–2 (0.7±0.7; $n=32$). Duration of postdischarge subphase $\bar{d}_p$ ($\bar{a}+\bar{r}$): 0.0–225.0 s (81.0±65.3; $n=50$). Duration of $\bar{a}$: 0.0–224.0 s (79.0±65.5; $n=50$). Duration of $\bar{r}'$: 0.0–3.0 s (1.6±0.7; $n=50$). Duration of worker oviposition: 1.0–7.0 s (3.0±1.8; $n=8$). Duration of queen oophagy: 1.0–7.0 s (3.2±1.6; $n=18$). Duration of food intake by the queen from cell: 1.0–5.6 s (2.1±1.2; $n=63$). Duration of queen oviposition: 1.2–5.8 s (2.7±0.9; $n=100$). Duration of queen oviposition in all cells of a batch: 40.0–435.0 s (227.2±85.1; $n=61$). Duration of $\bar{s}_p$: 1.0–7.0 s (1.8±1.1; $n=62$); of $\bar{s}_r$: 23.0–59.0 s (38.0±7.5; $n=77$); of $\bar{s}_s$: 35.0–95.0 s (63.8±63.0; $n=77$); of $\bar{s}_r+\bar{s}_s$ (individually measured cells): 73.0–140.0 s (101.3±14.6; $n=78$); of $\bar{s}_r+\bar{s}_s$ (all cells of a batch): 134.0–575.0 s (331.8±93.8; $n=61$). Total POP duration (from the appearance of first cell primordium to the end of the last operculation: 238–390 min (314.0±107.4; $n=2$).

Ethological features common to other studied stingless bee taxa

The comparison with bumblebees (BB) and honeybees (HB) are given when possible with 3 symbols (=: similar to; ≒: almost similar to; ≠: different from).

C1 – Peculiar temporal integration of the oviposition process (POP) with successive stages and phases never seen in any other social insects. C2 – Each cell built by several workers successively (≒HB), not through the continuous work of a single female (≠BB). C3 – Adjacent cells built independently (≒BB; ≠HB). C4 – Openings of completed cells narrowed (=collared) before food provisioning (≠BB, HB). C5 – Brood cells not reused (≒BB; ≠HB). C6 – Cells not reused for food storage (≠HB; ≠ or ≒BB). C7 – Cells not oviposited before completion (=BB; ≠HB). C8 – Only one adult emerging from a cell (≒HB; ≠BB). C9 – Cell wall not expanded after cell operculation (only exceptions *Frieseomelitta varia* and *Leurotrigona mülleri* queen cells) (Terada, unpubl.) (≒HB; ≠BB). C10 – Waxen cell walls removed by workers after larval cocoon spining (≒BB; ≠HB). C11 – Except *Trigona* (*Tetragonula*) *fuscobalteata*, a completed cell gradually attracting workers, and agitated attendants repeating fore-body insertions into the cell (≠BB, HB). C12 – Cells food-provisioned before ovipositions (≒, ≠BB; ≠HB). C13 – Workers withdrawing from the cell soon after food discharge (≠BB, HB). C14 – Exaggerated avoidance by workers of the approaching queen present (≒BB; ≠HB). C15 – Retinue gradually formed around the resting queen (≒HB; ≠BB). C16 – Rapid dashing followed by retreat repeated by each attendant facing the queen, involving occasional darting (≠HB; ≒, ≠BB). C17 – Licking queen by workers absent (≠HB; ≒BB). C18 – Trophallaxis among workers frequent (≒HB; ≠BB). C19 – Trophallaxis between queen and workers very rare (≒BB; ≠HB). C20 – Except *Melipona quadrifasciata*, the mature queen continuously beating wings (≠BB, HB). C21 – Feces provisionally deposited within the nest before being carried away (≠BB, HB).

Here we mention a queen-worker relation peculiar in some (probably many) stingless bees: the court size is often larger around younger queens (Fig. 4, left) than older ones (Fig. 4, right) just opposite to the royal courts around virgin and gravid queens in the honeybees (cf. Sakagami *et al.*, 1977*, p. 678 and Sakagami, 1982, pp. 381–4).

Ethological diagnosis of Plebeia droryana

Comparison of various ethological features of *Plebeia droryana* with other closely studied taxa is given below. Symbols and relevant references are as follows: *C* (*Cephalotrigona*, Sakagami *et al.*, 1964), *D* (*Duckeola*, Sakagami & Zucchi, 1968), *F* (*Friesella*, Sakagami *et al.*, 1973*), *L* (*Leurotrigona*, Sakagami & Zucchi, 1974*), *Lp* (*Lepidotrigona*, Sakagami & Yamane, 1987*), *M* (*Melipona*, Sakagami & Oniki, 1963; Beig & Sakagami, 1964; Sakagami *et al.*, 1965), *Ml* (*Meliponula*, Sakagami *et al.*, 1977*), *Mr* (*Mourella*, Wittmann *et al.*, 1991), *N* (*Nannotrigona*, Sakagami *et al.*, 1993*), *S* (*Scaptotrigona*,

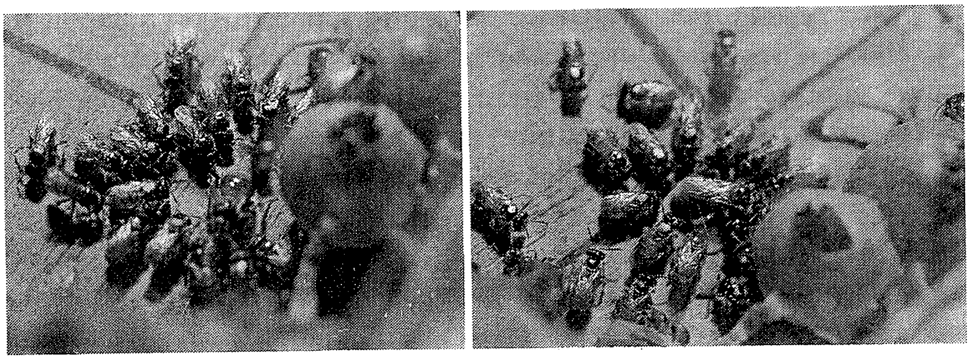

Fig. 4. Royal court formed around a young queen about 1 week after her nuptial flight (left), and that formed 2–3 weeks later around the same queen with enlarged metasoma (right) (1972, Ribeirão Preto). Workers are about 3 mm long, someones marked with lacquer.

SAKAGAMI & ZUCCHI, 1963), *Tl* (*Tetragonula* excl. *T. carbonaria*: SAKAGAMI *et al.*, 1983*; SAKAGAMI & INOUE, 1990*), *Tlc* (*Tetragonula carbonaria*: YAMANE *et al.*, 1995*), *Ts* (*Trigonisca*, SAKAGAMI & ZUCCHI, 1974*), *Tt* (*Tetragona*, SAKAGAMI & ZUCCHI, 1967), *X* (all other taxa), $^{\mathrm{t}}$ (partly), $^{\mathrm{p}}$ (requiring closer comparison).

Nest architecture: D1–Cells completely combed (≒*C*, *Lp*, *M*, *Mr*, *N*, *S*, *Tlc*, *Tt*), neither semicombed (≠*D*, *F*, *Ml*) nor in cluster (≠*L*, *Tl*, *Ts*). D2–Involucrum present (≠*D*, *F*, *L*, *Ml*, *Tl*, *Ts*; ≒*X*). D3–Queen cells larger than worker cells (≠*M*; ≒*X*). D4–Cells and pots opaque, not semitransparent (≠*L*, *Ts*; ≒*X*). D5–Nests never obligatorily subterranean (≠*Mr*; ≒*X*).

Behavior not involved in oviposition process: D6–Waste materials carried away on the wing, not thrown down from the nest entrance (≠*L*, *Ts*$^{\mathrm{p}}$; ≒*X*). D7–The queen not resting at a definitive place (≠*L*; ≒*X*$^{\mathrm{p}}$). D8–The queen not nearly always present on the combs (≠*N*; ≒*X*). D9–The queen walking started and stopped often abruptly, and remarkably rapid (≠*X*). D10–The queen not shaking antennae violently and incessantly, and not cruising excessively throughout the nest interior (≠*Ml*$^{\mathrm{p}}$; ≒*X*). D11–Rhythmic wing movements by the queen present involving vibration together with shaking (≒*D*, *F*, *L*, *Lp*, *M*$^{\mathrm{t}}$, *Mr*, *N*, *Tl*, *Tlc*, *Tt*) and neither rare (≠*M*$^{\mathrm{t}}$, *Ts*$^{\mathrm{p}}$) nor simply shaking (≠*C*, *M*$^{\mathrm{t}}$, *Ml*, *S*). D12–The queen only rarely taking oriented rest (≒*C*, *F*, *L*, *Lp*, *M*, *Ml*, *Mr*, *S*, *Tl*$^{\mathrm{t}}$, *Ts*), neither geopositively (≠*D*, *N*, *Tl*$^{\mathrm{t}}$, *Tlc*) nor geonegatively (≠*Tl*$^{\mathrm{t}}$, *Tt*). D13–Worker responses to the queen out of POP ritualized though involving agonism (≒*M*, *Ml*, *N*, *S*; ≠*X*, though occasionally with vestigial worker agonism in *Tl. pagdeni*). D14–The queen exhibiting actual or ritualized dominance (≒*M*, *N*; ≠*X*). D15–Feeding the queen by workers rare (≠*Lp*$^{\mathrm{p}}$; ≒*X*).

Food provisioning and oviposition process (*POP*): D16–Cell construction synchronous (type S$_{\mathrm{y}}$: ≒*D*, *F*, *L*, *Lp*, *N*, *Tlc*, *Ts*; in YAMANE *et al.*, 1995*, *L* is erroneously omitted from S_y), not successive (type S_c: ≠*X*). D17–POP batched exclusively (type B_e: ≒*D, F, L, Lp, N, S, Tlc*), not facultatively (type B_f: ≠*X*). D18–Food provisioning in cells synchronous (type D_y: ≒*Lp, Mr, N, S, Tlc*), not successive (type D_c: ≠*X* including *Tl*; in SAKAGAMI *et al.*, 1993*, *S* is erroneously placed in D_c). D19–During patrolling and arousal stages, the queen continuously cruising over the comb (type C: ≠*X*). D20–During arousal stage cell attendants not exhibiting exaggerated rocking movements (≠*Ml*^{p}; ≒*X*; unknown in *Tlc*). D21–Predischarge cell inspection by the queen frequent, neither rare nor absent (≒*M, Ml, S*; ≠*F, L, Lp, Mr, N, Tl, Tlc, Ts*) but never rhythmically repeated (≠*C, D, Tt*). D22–Predischarge worker behavior not simple (≠*L, Lp, M, Ml, Mr, Tl, Tlc*), with overt ritualized responses (≒*F, N, S, Ts*), whereas lacking repeated forebody insertions in cells (≠*C, D, Tt*). D23–Predischarge body insertions by workers not much replaced by intentional ones (≠*F, L*; ≒*X*; unknown in *Tlc*). D24–The queen never rushing on a particular cell attendant and seizing her (≠*Mr* and less overtly *F, M*^{t}; ≒*X*; unknown in *Tlc*). D25–The queen never violently tapping cell attendants (≠*F, M, Ml, Mr, Ts*; ≒*X*). D26–Workers persistently inserting forebodies in cells often being gnawed, tapped and strongly pushed away by the queen (≒*N*; ≠*X*). D27–Food discharge in the first cell in a batch occasionally evoked in the absence of the queen nearby (≒*Lp*^{p}, *Ml*^{p}, *N, Tlc*; ≠*X*, in SAKAGAMI *et al.*, 1993*, *N* was erroneously put in *X*). D28–Arousal of predischarge and predischarge agitations generalized (type Ag: ≒*Lp, Mr, N, S, Tlc*; not localized ≠*X*). D29–Number of food discharge per cell more than two (≠*L*; ≒*X*). D30–During discharge subphase the queen not making peculiar retreat from the cell (≠*M*; ≒*X*). D31–Postdischarge withdrawal of workers from cell distinct (≠*L*) and not slow (≠*D, Ml, S*; ≒*X*). D32–Metasomal contraction at food discharge conspicuous (≠*Ml*^{p}; ≒*X*). D33–Worker body insertion at each food discharge not prolonged (≠*Ml*^{p}; ≒*X*). D34–The queen not displaying repeated turnings around provisioned cells (≠*Lp*^{p}; ≒*X*). D35–Worker-born trophic eggs present (≠*D, F, L, Tl, Tlc, Ts*^{p}; ≒*X*). D36–Trophic eggs laid on the fresh comb, and not intimately linked with POP (≠*X*). D37–Postdischarge subphase of the first cell present (≠*D, F, L, Ts*) and virtually obligatory (≒*Lp, Ml, Mr, N, S, Tlc*), not facultative (≠*C, M, Tl, Tt*). D38–Many queen ovipositions not preceeded by cell inspection (≠*X*). D39–Queen oviposition made without exaggerated hind leg twitching (≠*D*; ≒*X*). D40–Duration of queen oviposition moderate (≒*D, F, Lp, Ml, Mr, N, S, Tl, Ts, Tt*), neither short (≠*C, L, Tlc*; in previous papers *L* was erroneously put in *X*) nor long (≠*M*). D41–Cell operculation started by a single worker with metasomal rotation (≠*F*; ≒*X*). D42–Differentiation of rotation and sidework subphases clear (≒*L, M, Ml, N, S, Tlc*), neither obscure (≠*C, D, Lp, Mr, Tl, Ts, Tt*) nor absent (≠*F*). D43–Duration of operculation moderate (≒*X*), not unusually long (≠*Tt, Ts*^{p}).

Discussion

Phenetic ethological similarity of Plebeia *with other taxa*

Table 2 depicts the relations of *P. droryana* to other ethologically analyzed taxa based on 15 diagnostic items after excluding from the diagnostic characteristics the probable autapomorphies (D3, D5, D7, D8, D9, D10, D15, D19, D20, D29, D30, D31, D32, D33, D34, D36, D39, D40, D41, D42: states shared by a single taxon, and D4, D6, D11, D12, D23, D26, D43: states shared by only two taxa).

Though tentatively some phyletic and non-phyletic ethological similarities among observed taxa are mentioned: 1−The highest features shared among *Plebeia*, *Nannotrigona* and *Scaptotrigona* may reflect the similar POP sequence due to their phyletic affinity. 2−The relatively high sharing rate between these taxa and very peculiar *Melipona* suggests their phyletic affinity, despite many conspicuous differences (MICHENER, 1990; CAMARGO & PEDRO, 1992). 3−Low sharing rates between *Plebeia* and the taxa that developed, probably independently, semicomb or cluster cell arrangement (* in Table 2) may involve secondary ethological modifications. 4−The relatively high sharing rates be-

Table 2. The number of items (given in the ethological diagnosis), shared by *Plebeia* and various other taxa arranged in the descending order.

Taxon groups	Distribution	Taxon	Number of items shared by *Plebeia* and other taxa**	
			n	% (100×*n*/15)
P	N	*Nannotrigona*	14	93.3
P	N	*Scaptotrigona*	12	80.0
T	O	*Lepidotrigona*	11	73.3
T	Au	*Tl. carbonaria*	9	60.0
X	N	*Melipona*	6	40.0
X	Af	*Meliponula**	6	40.0
P	N	*Mourella*	6	40.0
T	N	*Cephalotrigona*	5	33.3
T	N	*Tetragona*	5	33.3
X	N	*Leurotrigona**	4	26.6
T	N	*Duckeola**	4	26.6
P	N	*Friesella**	3	20.0
X	N	*Trigonisca**	3	20.0
T	O	*Tetragonula**	2	13.3

Taxon groups: P: *Plebeia complex*; T: *Trigona complex*; and X: Other groups.
Distribution: N: Neotropical; O: Oriental; Au: Australian; and Af: African.
* Brood cells arranged in semicombs or in cluster, not in combs.
** Excluding those items of which features were common to all taxa compared, except in 2 taxa (see items D4, D6, D11, D23, D26 and D43) or in 1 taxon (all other items, e.g., D3, D5, etc.).

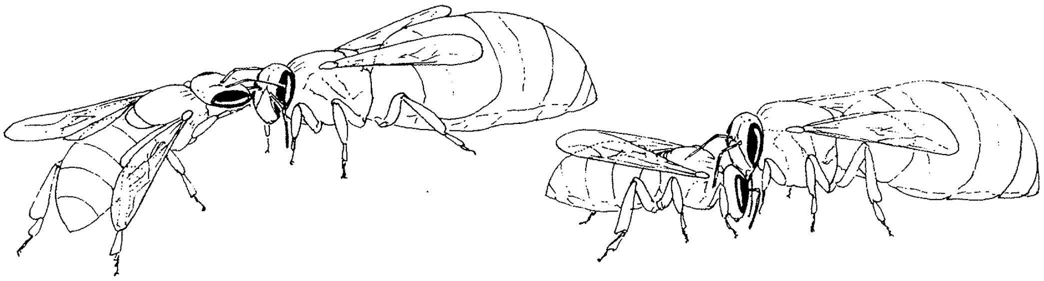

Fig. 5. The queen-worker interaction in *Trigona* (*Tetragonula*) *pagdeni*. Worker is darting at the queen (left) and then crouches in the queen's front (right) (cited from SAKAGAMI *et al*., 1983*).

tween *Plebeia*, *Lepidotrigona* and *Tetragonula carbonaria* indicate that the latter two Indopacific taxa retain more phyletic relatedness to the *Plebeia* complex than some Neotropical sisters, such as *Cephalotrigona*, *Tetragona* and *Duckeola*, which have deviated more from the ancestral *Trigona* complex. 5 – *Tetragonula carbonaria* is very interesting, because *Tetragonula* is probably the most deviated branch in the *Trigona*-complex, but ethologically *T. carbonaria* still retains strong phyletic similarity to the *Plebeia* complex. The relation between *T. carbonaria* and other *Tetragonula* is in a sense comparable to that between *Plebeia* s. str. and some other *Plebeia*, such as *Friesella*, though the phyletic situation is opposite: *T. carbonaria* is exceptional within *Tetragonula* for its ancestral (plesiomorphic) traits, whereas *Friesella* is exceptional within *Plebeia* for its ethological apomorphy. 6 – Many Neotropical taxa of the *Trigona* complex abandoned the ritualized queen-worker interactions probably except some *Geotrigona* and *Tetragonisca*. The same applies to *Tetragonula* including *T. carbonaria*. Nevertheless, such ritualization remains very vestigially in some worker responses to the queen as shown by darting occasionally followed by weak crouching in *T.* (*Tl.*) *pagdeni* (Fig. 5).

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