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**Additional Observations on the Habits of the Cleptobiotic
Stingless Bees, the Genus *Lestrimelitta* Friese
(Hymenoptera, Apoidea)¹⁾**

By

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(With 6 Text-figures)

Among all stingless bees, the genus *Lestrimelitta* Friese, including two Neotropical species, *L. limao* (Smith) and *L. ehrhardti* Friese and one Ethiopian, *L. cubiceps* Friese, occupies an outstanding position, morphologically by the peculiar ratios in antennal segments, the unusually long worker malar spaces, and, first of all, by the very incomplete development of worker corbiculae, and biologically by its cleptobiotic mode of life. Previous information concerning their habits, all dealing with *L. limao*, was reviewed by Schwarz (1948), of which two aspects were specially noteworthy: Its cleptobiosis³⁾ and its peculiar nest entrance.

It has been reported repeatedly that *L. limao* frequently attack the nests of various other stingless bee species, robbing honey, pollen and building material. But the opinions among the writers differ as to whether this habit is obligatory or not (Cf. Schwarz, 1948; Nogueira-Neto, 1949). Friese (1931) stressed its obligatory nature, whereas Schwarz, though admitting frequent execution of robbery, doubted such obligatory cleptobiosis, chiefly for the two following reasons: 1. Some nests were too prosperous and persisted for too many years in the same place for them to survive solely at the sacrifice of other species. Further, v. Ihering (1903) could rear one colony of *L. limao* in a place where no forest existed, hence no other

1) Joint contribution from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan (No. 606) and Departamento de Zoologia, Faculdade de Filosofia, Ciências e Letras, Universidade do Paraná, Curitiba, Paraná, Brasil (No. 151).

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3) Exactly stated, this species corresponds both to clepto- and lestobiosis in the definition by Wheeler (1923). It is lestobiotic because it attacks the nests, not the foraging parties of other species, but also cleptobiotic because its nest is not constructed within or near the victim nests.

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stingless bee nests were there to be attacked. 2) The honey of *L. limao* has often been reported poisonous. This is difficult to understand, if it lives exclusively depending on the other species.

But further observations, chiefly made in Brazil, seem to reveal the obligatory cleptobiosis. At least, the observations of their robbery have increasingly been accumulated, while hitherto no one had collected this species on flowers (Various personal communications from Brazilian colleagues, especially Prof. W.E. Kerr, Prof. Pe. J.S. Moure, CMF and Dr. P. Nogueira-Neto). Kerr (1951) added two new observations concerning the robbing habits: 1. Robbing workers transfer the pollen storage of victim colonies in a paste by means of an acid secretion from the mouth and carry back such paste-like pollen in their stomach, not in the corbiculae. 2. The robbing party can work with little resistance by victim colonies, members of which are *frightened* by the strong lemon-like odour emitted by the thieves. Further, Araujo (1958) revealed in his observations on the African congener, *L. cubiceps*, that this species also took most probably all, of the food and building material by attacking the nests of *Trigona* (*Hypotrigona*) *braunsi* Kohl (= *Hypotrigona* (*Hypotrigona*) in Moure, 1961).¹⁾

Another peculiar feature of *L. limao* is its nest entrance. All previous writers reported the elaborated construction of its nest entrance. But two different types seem to exist. Holmberg (1887) and Silvestri (1902) noted the entrance architecture as a sponge-like mass provided with several elongate tubes on the surface. On the other hand, all other writers called attention to the single, elongate entrance tube extending up to 35 cm, often provided with stalactite-like blind protuberances on the underside. As the observations of both Holmberg and Silvestri were made in the southern parts of the distribution of the species, Schwarz suggested a possible architectural difference within its vast range.

At any rate, the accumulation of more information is obviously needed in order to clarify the bionomics of this interesting group. The present work is an outcome of our observations made in the State of Paraná, Brazil, which are mostly fragmentary but, we believe, worthwhile to record.

Before going further, we would like to express our cordial thanks to Prof. Pe. J.S. Moure, CMF, Departamento de Zoologia, Faculdade de Filosofia, Universidade do Paraná, Curitiba, Prof. W.E. Kerr, Departamento de Biologia Geral, Faculdade de Filosofia, Rio Claro, and Dr. P. Nogueira-Neto, Departamento de Zoologia, Faculdade de Filosofia, São Paulo, for their kind encouragement and valuable suggestions for our work, to Prof. B. L. Lucas de Oliveira for her information concerning the robbing tactics of *L. limao*, and to Messrs. A. Wischral and P. Cunha, for their generous permission to make observations in their fazendas.

I. *Lestrimelitta limao* (F. Smith)

1) In the present paper, the supraspecific system follows that of Moure (1961) except for citations, in which the Mourean system is mentioned in parentheses.

1. 1. *Occupation of the nests of Melipona quadrifasciata quadrifasciata* Lepeletier.

Beside its robbery, it is probable that *L. limao* often invades the nests of other stingless bee species, drives out the owners and usurps the nests, including deposited food. Friese (1931) cited the observations by Ehrhardt made in São Paulo as follows: Die Spürbienen gehen nach dem Ausschlüpfen der jungen Brut und nach dem Erstarken des Volkes auf Suche nach einem in guter Entwicklung stehenden Baumnest einer anderen *Trigona*-Art (z. B. *Tr. dorsalis*, *bipunctata*, *tubiba*)¹⁾...., die rechtmässigen Bewohner samt Brut zu vernichten und Besitz von den fertigen Waben samt Vorräten an Honigtöpfen, Pollen, Harz und Wachs zu ergreifen. Schwarz (1948) also cited the observation made by Baker in San Felix, Venezuela, on the invasion by *L. limao* of the nest of *Melipona favosa favosa* Lepeletier. The following observations were made in the vicinity of Curitiba.

Case 1: The invaded colony of *M. q. quadrifasciata* had been kept by Mr. A. Wischral in a wooden trunk cut both at top and down and located horizontally about 2 m above soil surface. The nest of *L. limao* was also situated about 3 m high, approximately 10 m apart from the victim nest. According to the owner, the invasion began about one week before the inspection of the nest by one of us (S.L.) on 30 May, 1963. On that day, the invaders had already constructed the entrance tube of about 4 cm in length and 2.5 cm in the maximum outer diameter, made from dark cerumen mixed with finest sand particles. When the nest was opened, a strong lemon-like odour dominated the interior, in which about 100 workers of *L. limao* were found, about 30 on or between involucrum, while about 70, together with one male, on pollen pots, taking pollen and rebuilding involucrum. About 200 *M. q. quadrifasciata* workers, mostly still young and unable to fly, still remained. They were found partly on involucrum but mostly on brood combs, together with their gravid queen, who was excitedly crawling to and fro on a comb. Some *M. q. quadrifasciata* workers attempted to attack *L. limao* workers by biting the latter's mesosoma and wing bases. But *L. limao* workers were more agile in counter-attack and killed many *M. q. quadrifasciata* workers. No old *M. q. quadrifasciata* workers were found. It is plausible that most of them abandoned the nest. Mr. Wischral told to S.L. that he noticed one *M. q. quadrifasciata* worker, overnighting on the outer surface of nest entrance.

Considering the relatively small number of *L. limao* workers in the nest, it is probable that this case indicates the incipient stage of the swarm migration by *L. limao* from the original colony.

Case 2: This case also occurred in the same fazenda. The attacked colony of *M. q. quadrifasciata* had been reared in a wooden box of about 31 cm long, 23 cm wide and 24 cm high, located 2.2 m above soil surface. The colony was

1) According to Schwarz (1948), *T. dorsalis* is identical to *T. (Scaptotrigona) postica* Latreille, which, together with *bipunctata* and *tubiba* enters *Nannotrigona (Scaptotrigona)* in the system by Moure.

invaded by a *L. limao* colony, which lived there 3–4 years but recently abandoned the nest for an unknown reason. The colony was quite prosperous and left a very beautiful entrance architecture as shown in Fig. 1. The entrance architecture was made from the cerumen mixed with finest sand particles, covering a lower corner of the box, where the entrance hole was perforated, and hanging further downwards. The whole dimensions were 36 cm wide, 12 cm thick and 60 cm. high, that is, the largest entrance structure so far known in the nests of this species, or, probably of all stingless bees.

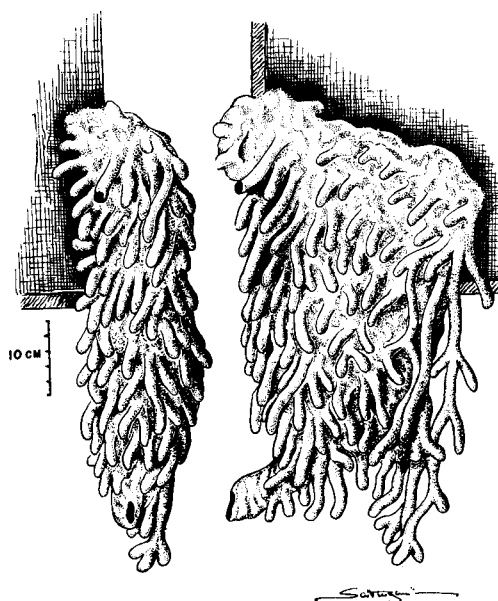


Fig. 1. An enormous entrance architecture in an abandoned nest of *Lestrimelitta limao*. Left: Profile view, Right: Frontal view. The entrance tube seen below, and one broken protuberance above.

The surface was provided with numerous enlongate protuberances, that is, like those illustrated by Silvestri but incomparably more numerous and far more lengthened. The protuberances were about 1.5–1.8 cm in diameter and mostly 4–12 cm in length, but some especially those at the rear part of the architecture, were remarkably long, even exceeding 40 cm, irregularly ramifying or connecting themselves one to another. They were all blind sacs except one, apparently accidentally broken (Fig. 1, above).

The true entrance tube took its definite form only at the end part where it formed a laterally compressed tube of about 13 cm long, 5 cm high and 4 cm wide, with the entrance hole of 1.2 cm wide and 1.8 cm high, which was situated about

25 cm apart from the entrance hole of the wooden box. There were a few short blind protuberances on the underside of the tube. Summarizing, the entrance architecture of this nest possessed the characteristics of both types described by Holmberg and Silvesitri (in the possession of numerous protuberances on the surface) and by the other writers (in the elongate entrance tube provided with protuberances on the underside), but greatly exceeded both in its extreme complexity, suggesting an architectural climax reached by this species.

1. 2. *Repair and development of entrance architecture*

One nest of *L. limao* was discovered on 5 April, 1962 in a hollow tree in Passeio Público, Curitiba. The nest entrance was situated 94 cm above soil surface, where the diameter of the tree was 58 cm. As the nest site was quite near Departamento de Zoologia, we could visit there frequently, usually after lunch time, and take notes until the end of June.

The entrance structure was seriously broken at the discovery of the nest. Thereafter, the process of repair and development was continually observed. Because the nest was situated in a place which received frequent interference by men, the partial destruction of the architecture happened frequently in spite of our efforts to minimize the attentions of other persons at observation. Consequently, the entrance did not develop to the elongate tube within the observation period. Fig. 2 shows the process of repair and development during a relatively stable period, in which destruction did not happen. After receiving damage on 26 April, the surface cover of the architecture was gradually repaired as seen in the figures (IV 29-V 2). The repairing speed was not very rapid compared to other reports (for instance, Rau, 1933), probably caused by adverse weather conditions. Once the repair was more or less completed, some general trends dominated throughout the observation period as follows: 1. Formation of numerous cupola-like protuberances of 1.0–1.5 cm both in diameter and height over the surface, which daily changed their form, size and position, often disappearing and again appearing. 2. Formation of several large protuberances such as a large block at the lower lefthand in the figures and a few elongate tubes of 2–4 cm in diameter and 2–8 cm in length. The constancy of these structures was quite variable. Some, for instance the large lower block and elongate upper and lower tubes at the right-hand, persisted throughout the observation period. On the other hand, other tubes or their rudiments repeatedly appeared and disappeared. 3. The entrance holes, too, frequently changed their form and position. Often a new entrance appeared at the end of a hitherto closed tube, while previous ones were closed. 4. There was a general tendency to keep the margins of the entrance holes in round and smooth contour, which was seen even on 2 May, before the completion of repair. 5. All these entrance holes were closed at night, either completely or leaving only a very small hole of up to 8 mm in diameter. 6. Throughout the period, the entrance architecture always remained as a thin and soft layer. Often deforma-

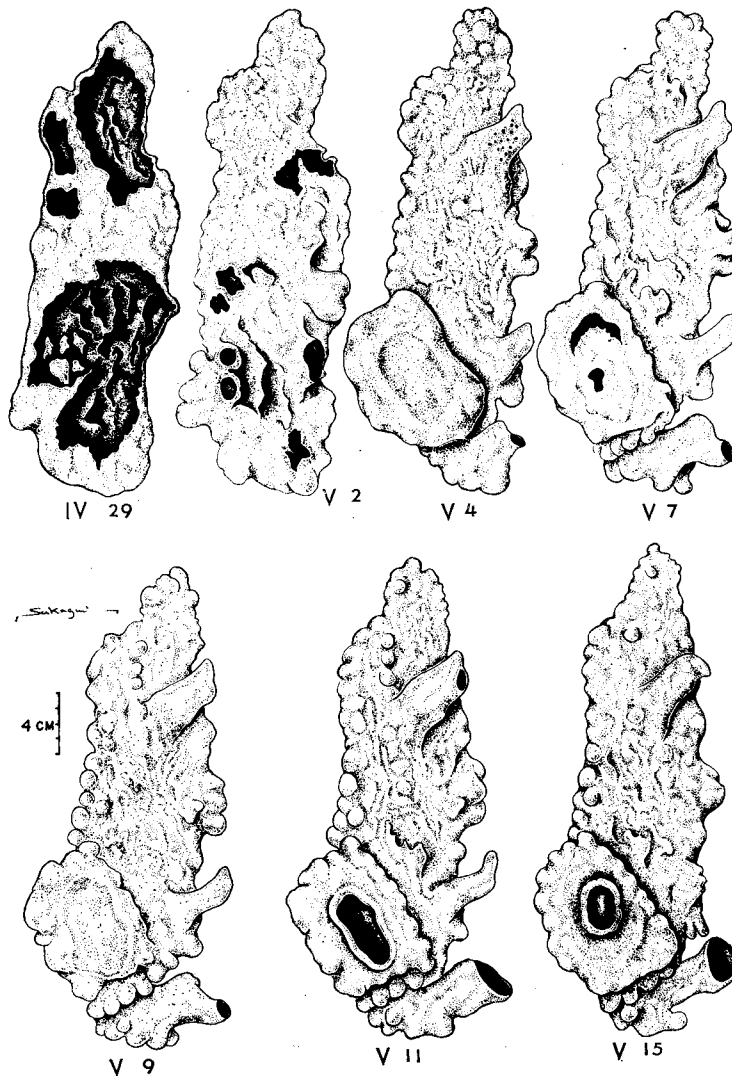


Fig. 2. Repair and development of entrance architecture in a continuously observed nest of *L. limao*.

tions due to the activities of bees working beneath were visible from the outside.

These trends were also detected in the other periods, though less obvious because of repeated destructions, and indicate the relatively poor integration of rather independent contributions by each worker to the whole process. When, for

instance, the surface cover was seriously damaged, the repair of the exposed surface was relatively rapid, probably because all individual activities took the same direction, nevertheless each worked rather independently. Once such a stage was passed by, however, the subsequent process was characterized by the lack of integration of individual activities, indicated by frequent disappearance and reappearance of protuberances and rudiments of tubes, as well as changes of entrance holes. Under undisturbed conditions, the next steps may ultimately appear in spite of such loose integration, that is, either the number and length of protuberances would increase, or a single main tube would be prolonged and consolidated. The first trend appears to prevail in the nests reported by Holmberg and Silvestri, while the second appears in those by other writers. Apparently, these two trends are characteristic of the entrance architecture of *L. limao*, though still cannot determine whether the difference in relative prevalence of both trends is, as suggested by Schwarz, geographic or not. In the nest observed by us, however, the further advance of the process did not take place, caused by frequent human interference. Under such a circumstance, the integration of activities of each bee to the whole pattern was probably disturbed so that they could not take a common direction, to which rather independent individual contributions are to be focused, because such direction has always been eliminated at the incipient stage.

1. 3. Behaviour at nest entrance

Beside the repair and development of entrance architecture, the behaviour of foraging and guarding bees was continuously observed. The foraging intensity was estimated by counting the number of returning bees during five minutes. Air temperature, wind classes (0–3) and insolation (good, weak, cloudy) were also measured before the counting. All observations were carried out within 12:20–13:00, usually at 12:30. Curitiba lies near the southern limits of the wide distribution range of *L. limao*. Considering the relatively high altitude of the city (about 900 m) and the season in which observations were carried out (autumn to early winter), the results presented in Fig. 3 could be regarded as showing the limits of flight activities under unfavorable weather condition. Obviously both air temperature and insolation play important roles. When the air temperature was either above 22°C or below 17°C, flight activities seem, respectively, to be released or inhibited irrespective of insolation. On the other hand, when the air temperature ranged between 18–21°C, insolation markedly affected the flight activities. The influence of wind velocity could not be estimated exactly, for relatively windy days were usually cold and less insolated. But the data on 26–27 April suggest that mild wind does not disturb the flight activities, as long as temperature and insolation lie within favorable ranges.

A clear mutual mimetic tendency (Armstrong, 1951=allelomimetic reaction, Scott, 1950) was seen among the returning bees. Many returning bees did not

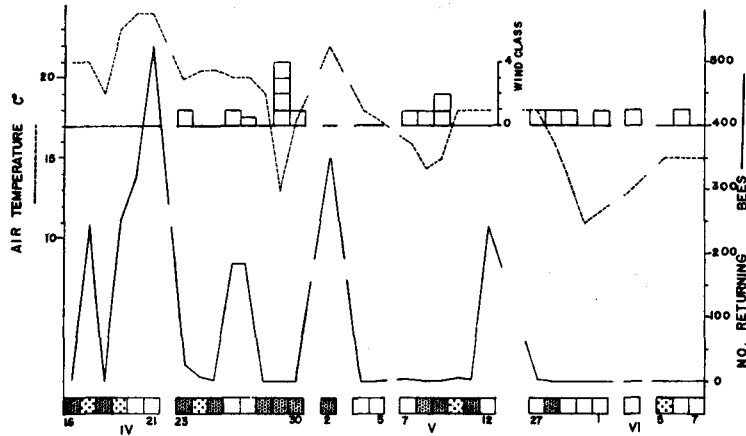


Fig. 3. Influence of weather conditions on the flight activities. Blocks at bottom show insolation. White: good, sparsely dotted: weak, densely dotted: cloudy. Absence of block means the lack of observation.

immediately enter the nest, staying for a while in the wing about 10–20 cm apart from the nest entrance. When the flight activities were quite intensive, such delay soon resulted in the formation of a swarm consisting of 20 to 30 bees, each keeping approximately the same distance from one another. Thus the swarm behaved in a manner similar to that found in schooling fishes, always keeping the group integration even if drifted to and fro as a whole by a gentle breeze. Once one of such floating bees decided to alight on the entrance, she was immediately followed by the other bees. Thus the frequency of landing bees showed a marked discrete pattern with intervals of 1–2 minutes. Many returning bees carried back building material in their corbiculae, which was the same as that by which entrance architecture was built up, that is, pale brownish cerumen. The sources of this material could not be determined. It was also not examined whether or not some returning bees contained stollen pollen paste in their stomach.

The guarding bees were sitting, side by side, on the inner margins of the entrance holes, or, on warm days, on the outer surface of the entrance architecture. The mild temperament of these professional pirates to human observers, reported in previous records (*Cf.* Schwarz, 1948), was also seen in this nest. When disturbed by means of a pencil or finger, the bees sitting on the surface stretched their antennae and occasionally also fore-legs to the stimulus. This was almost the unique positive attitude against such interference. Occasionally, they pushed these appendages a little further, but usually retreated without subsequent resistance. When the same stimulation was applied to the bees sitting on the inner margins of the entrance holes, they usually simultaneously retreated to the interior, though not so harmoniously synchronized as in *Nannotrigona* (*Nannotri-*

gona) *testaceicornis* (Lepeletier) (Sakagami & Zucchi, unpub.). One of us (S.F.S.) once noticed a bee approaching and touching his hair, but without alighting or biting as frequently is done by some aggressive species. According to Michener's classification (1961), *L. limao* indubitably enters the group *not aggressive*.

Such a mild disposition was also seen in their attitude to the returning nest mates, which were inspected only slightly by the stretched antennae. Further, on warm days, several honeybee workers and usually more numerous workers of *Plebeia* (*Plebeia*) *emerina* (Friese) were observed on the surface of nest architecture, eagerly gathering there building material. When encountering such *thieves*, *L. limao* showed no marked threatening reaction other than a weak chasing with stretched fore-legs. No severe combat was released because the thieves used to escape a few centimeters from such mild chasing. The frequent visits of *P. emerina* are interesting, for this species is the principal victim of *L. limao* in and near Curitiba. It would not always be possible to assume that some workers of *P. emerina* working on the nest were not thieving but merely regaining their legitimate property. Moreover, the fact that they are working on the nest is remarkable, because the place was saturated by the strong lemon-like odour characteristic of *L. limao*, which as mentioned in the introduction, the odour to conquer the victim nests. Probably the reaction of *P. emerina* to this odour would be quite different within and outside their nests. Or it is assumed that *L. limao* emits a stronger odour at robbery than in the nest.

When the air temperature was higher than about 20°C, the fanning behaviour was observed at or near the entrance. The fanning posture was the same as that observed in other stingless bees and *Apis cerana* Fabricius, that is, directed against the entrance, not towards the latter as in *Apis mellifera* Linné (Sakagami, 1960). The metasoma was slightly raised and the wing movements were rather weak, noiseless and intermittent.

In contrast to the other stingless bees, this species has a trait of accumulating the waste material below the nest entrance, not carrying it away in the wing. The dumped material included dead bodies of broods and adults but mostly consisted of the building material similar to that applied to the entrance. We repeatedly observed that one bee or more appeared at the entrance, holding the building material between their mandibles, and threw it down, either simply from the entrance or after walking down 5 to 10cm on the trunk. This means a very uneconomical use of the material in this colony. The same material was constantly brought in the nest by foragers and, at the same time, thrown away by house bees. Moreover, it was repeatedly observed that some bees walked down the trunk to the accumulated dumped material and returned to the nest bringing in their corbiculae the material once thrown away by their nest mates.

Such co-existence of oppositely directed work is frequently seen in insect societies (for instance, Geotsch, 1935). The same tendency was found, as described above, in the repair and development of the entrance architecture. This

leads to the assumption that in insect societies there are many, if not all, processes which are accomplished by relatively independent activities of each individual. One of the most remarkable facts in the insect societies is that, in some kinds of work, the whole process is ultimately accomplished in harmony, although no particular communication mechanism is detected which may adjust oppositely directed acts and coordinate each individual contribution to the whole pattern. Recently Wenner (1961) proposed to interpret such events, not in terms of simple stimulus-response arc, but by means of a stochastic model such as Markov's process. One of us (S.F.S.) agrees with this opinion with a reservation. While such lack of coordination is obvious to anybody who has some experience with the intimate life of social insects, nobody can deny the occurrence of diverse types of communication, either as very advanced types as shown by v. Frisch's contributions, or as less perfect types as seen in ants (Goetsch, 1933), and the probable occurrence of still undiscovered communication systems. Perhaps insect societies can best be expressed as a water mass consisting of some stochastic processes as suggested by Wenner, in which some more solid, that is, better integrated systems are floating, either as perfectly crystallized systems or as less perfect masses.

1. 4. *Unsuccessful (?) occupation of the nest of Plebeia (Plebeia) emerina (Friese)*

Our observations of the nest of *L. limao* in Passeio Público were obliged to be suspended by an unexpected event. On 15 May, two other nests of stingless bees were found in another hollow tree less than 100 m apart from the nest of *L. limao*: One nest of *Trigona (Tetragonisca) jaty* Smith on the northern side of the tree about 1.5 m above the soil surface, and one of *P. emerina* on the opposite side about 0.6 m above the surface. Thereafter, these two nests received our continuous observations. Some workers of *T. jaty* always visited the nest of *P. emerina*, taking the hovering posture in front of the nest. Such *watching* is a trait very characteristic of this species and often changes to robbery or even to the extermination of the nest, in spite of its midget appearance and relatively mild disposition to human observers. But in the present case, *T. jaty* did not develop any vigorous attacks against *P. emerina*, nor did *L. limao* attack either colony until 25 June, 1962. The subsequent observations are chronologically arranged as follows:

VI 25. 13:20. The nest of *L. limao* had been abandoned. The entrance area was visited by 3-4 *P. emerina* workers (probably the individuals belonging to a colony different from that concerned here. There were about five colonies of this species in Passeio Público) and a few phorid flies. Only one *L. limao* worker was seen flying around near the entrance. (Thereafter, this nest site was never recolonized by any stingless bees. All material forming entrance architecture was gradually carried away by *Apis mellifera* and *Plebeia emerina*). The *P. emerina* nest had been occupied by *L. limao*. About 50 workers were sitting in or near the entrance. Through the narrow entrance of approximately 9 mm in diameter, many *L. limao* workers were seen under the surface cover. No trace of *P. emerina*

workers was detected in and near the entrance. About 5-6 workers of *T. jaty* were hovering in front of the entrance as usual. On the ground one couple of *T. jaty* and *L. limao* was rolling, severely grasping each other.

14: 30. More or less similar situation. Formation of cupola-like swellings characteristic of *L. limao* was beginning on the entrance surface. *L. limao* workers guarding the entrance were in a quite excited state, stretching antennae and fore-legs rather more vigorously than usual against our approach. About 5-6 *T. jaty* workers continued to hover in front of the entrance. On the ground, five couples of *T. jaty* and *L. limao* in combat and about 30 dead bodies of *T. jaty* were found. No *Plebeia* worker, either living or dead, was seen in and near the entrance nor on the ground.

VI 26. 6: 00. The cupola-like swellings of the entrance area had disappeared. The entrance hole had decreased to 3 mm. Several *P. emerina* workers appeared when inspected. About 6 dead workers of *T. jaty* still remained on the ground but no dead of *L. limao* nor *P. emerina* was found.

9: 10. The entrance hole was still only 8 mm in diameter, guarded by several *P. emerina*.

17: 30. The entrance was again guarded by about 20 *L. limao* workers, seven of which carried heads, with or without mesosoma, of *T. jaty*, which still firmly grasped with their mandibles various body parts, mostly wing bases of *L. limao*. All guarding bees showed the mild reaction characteristic of the species against our approach. About 2-3 *P. emerina* workers were flying to and fro near the entrance. One of them attempted to enter the nest but was immediately driven away by *L. limao*. The surface architecture again showed cupola-like swellings.

19: 30. *L. limao* workers were still found at the entrance area when the closed entrance hole was artificially opened.

VI 27. 10: 00. Similar situation. The entrance architecture was provided with three holes, each guarded by about 10, 20 and 20 *L. limao* workers respectively. The cupola-like swellings were seen as on the last day. Five guard bees still carried heads or fore-bodies of *T. jaty*. From the position of these dead *T. jaty*, it was verified that all five bees were those observed on the last day. About 20 *P. emerina* workers were straying near the entrance and one worker of the same species was carrying aimlessly a dead *T. jaty* on the ground.

12: 40. Similar situation. About 20 *L. limao* workers guarded the entrance, of which four were identified as those observed at 10:10 by still attached *T. jaty* heads. About 3-4 *T. jaty* workers were hovering in front of the entrance. One *P. emerina* worker attempted to enter the nest but was rejected immediately by *L. limao*.

VI 28. 12: 45. No trace of *L. limao*. The nest was again guarded by *P. emerina*. The entrance was narrowed. *T. jaty* continued to hover.

14: 40. No trace of *L. limao*. Departures and returnings of about 50 *P. emerina* during 5 minutes. The entrance was guarded by *P. emerina*. The cupola

like swellings disappeared and the entrance hole took the narrow round shape characteristic of the legitimate owners.

.....

VII 13. 14: 00. The nest was again guarded by *L. limao* as in the previous case. About 3-4 *P. emerina* workers were flying near the entrance but could not enter the nest. 16: 00. Same situation. 20: 00. Nest was completely closed but *L. limao* workers were seen when exposed artificially.

VII 15-18. The occupation by *L. limao* continued. Little flight activities due to low temperature ($\pm 15^{\circ}\text{C}$).

VII 19 and thereafter. Again *L. limao* disappeared. The entrance was guarded by *P. emerina* workers. Thereafter no trace of *L. limao* was observed and the colony continued to live normally.

Obviously, this record shows the invasion by *L. limao* inhabiting the nest continuously observed by us of the nest of *P. emerina* which was also under observation. But it is strange that, after the first invasion, *L. limao* and *P. emerina* alternately guarded the nest, which is summarized: VI 25: *L*, VI 26: At first *P*, then *L*, VI 27: *L*, VI 28-VII 12: *P*, VII 13-18: *L*, VII 19-: *P*, or *L1-P-L2-P-L3-P*. It is conceivable that *P. emerina* survived throughout this alternation, only driven away from the entrance area when the latter was dominated by *L. limao*. Otherwise, it is difficult to explain why the colony could normally continue to live after 19 July. On the other hand, it is not easy to give a reasonable interpretation to the intermittent occupation of the nest entrance by *L. limao*. Three possible explanations are given as follows, though none of them is decisive. A: Co-existence of both species within the nest. B. Double invasion from two independent colonies of *L. limao*, and C. Initial unstable phase of nest site selection by scout parties issued from the same colony. The first explanation is relatively plausible with respect to *L1-L2*, which occurred within a brief interval. If this is the case, the occupation of the entrance by *P. emerina* in the morning could be explained by the retreat of invaded *L. limao* into the interior of the nest caused by low temperature, to which *L. limao* is apparently more susceptible than *P. emerina*. On the other hand, *L1-L2* can be interpreted equally by the third explanation. Corresponding to the appearance of migration urge, the colony divided into several groups, each procuring a suitable site. One of them occupied the nest of *P. emerina* but abandoned it and relocated at another site, while another party, which had occupied another site, changed to this site but again abandoned it. The issue of several scouting parties at the incipient stage of swarming is reported by Lindauer (1951) in *Apis mellifera* and by Nogueira-Neto (1954) in stingless bees, including the colony fission caused by the strong attractions to the two different sites. These were observed in the swarming, not in the colony migration. But the same event could happen in the latter case, too. As to the relation *L2-L3*, the second and third explanations can be applied, but both are less plausible. The interval was too short to be regarded a migration process of

one and the same colony, while too long for the second explanation, because the chance of such coincidence seems to be very small in *L. limao*, of which nest density is low, apparently caused by its peculiar mode of life.

As to the fate of *L. limao* workers which once occupied the *P. emerina* nest but later disappeared, migration to the other site is a more plausible explanation than death by aging or that they were killed by *P. emerina*, because no dead bodies of *L. limao* were found near the nest, except those killed by *T. jaty*.

The event was complicated by the interference by *T. jaty*. But this is understood from the characteristic trait of the latter species mentioned above. Indubitably, constant watching by *T. jaty* of the *P. emerina* nest had to continue after the occupation by *L. limao*, resulting in severe combats as noted above. Although *L. limao* is quite mild to human observers, and it uses the odour as the principal weapon to conquer other colonies, it is highly probable that this professional robber can fight vigorously if necessary, as suggested in the observation by Schwarz (1948).

1. 5. *Some notes on the robbing habits (information by B.L. Lucas de Oliveira)*

We would like to add here a brief note on the robbing behaviour of this species in Curitiba, mainly based upon the personal communication by Prof. B.L. Lucas de Oliveira, who frequently observed the attack of *L. limao* on one colony of *P. emerina*, the principal victim in this area, kept by her. When this colony had previously been placed in the campus of Faculdade de Farmacia, it had not been robbed. But after it was transferred to her parent's house, it suffered the robbery by *L. limao* at intervals of 2 to 2.5 months for a few years until its sudden disappearance in 1963. This suggests that a definite colony of *L. limao* visited the victim colony regularly, until it succumbed or changed to a new site.

In each tour, the attack was made more or less in a similar manner. At first *P. emerina* showed a little resistance to the robbers but it ceased soon after. The robbing bees used to occupy the entrance tube. They inhibited the entry of *P. emerina* workers returning to the nest, allowing only their nest mates. Further, *L. limao* nibbled the entrance tube continuously until the latter became a thin and fragile remnant, the trait reported also by Michener (1946) when *L. limao* attacked *Trigona* (*Nannotrigona*) *testaceicornis perilampoides* Cresson (= *Nannotrigona* (*Nannotrigona*) in Moure, 1961) in Barro Colorado Is., Panama Canal Zone. The attack usually continued during 2-3 days and could continue further if not artificially inhibited.

Prof. Lucas de Oliveira kept one colony each of *Melipona nigra schenckii* (Gribodo) and *Plebeia* (*Plebeia*) *remota* (Holmberg) in the same place. *L. limao* occasionally attempted to attack these colonies, too, but never succeeded because of the effective defense of the former, and by the very narrow entrance hole (only 3 mm against 8 mm in *P. emerina*, measured by S.F.S.) surrounded by hard resinous walls in the latter.

II. *Lestrimelitta ehrhardti* Friese

L. limao is the species with a wide distribution range, extending from southern Mexico to southern Brazil and Northern Argentina, and, though not quite abundant everywhere, is recorded from many localities within its range. On the other hand, *L. ehrhardti*, the other Neotropical species, is extremely rare, so far recorded only in two localities, both in Brazil: Uberaba, Minas Gerais (2 workers) and São Paulo, S.P. (1 male) (Schwarz, 1948). Therefore it was fortunate that one nest of this species was discovered at Santa Quitéria, Município de Castro, Paraná.

This was another instance of the invasion of *Lestrimelitta* of the nest of *Melipona quadrifasciata quadrifasciata*. According to Mr. P. Cunha, in whose fazenda this nest was found, the invasion began a few days before the first visit by one of us (S.L.) on 13 November, 1961. The nest site was a hollow Ipé tree. At about 90 cm above soil surface, where the diameter of the tree was 68 cm, there was a large outer hollow of approximately 24×39 sq.cm, which was connected to the inner hollow, in which the nest was located, by means of a narrow canal used by *M. q. quadrifasciata* as the entrance canal. On 13 November, the nest entrance characteristic of *M. q. quadrifasciata* still remained consisting of radiating ridges

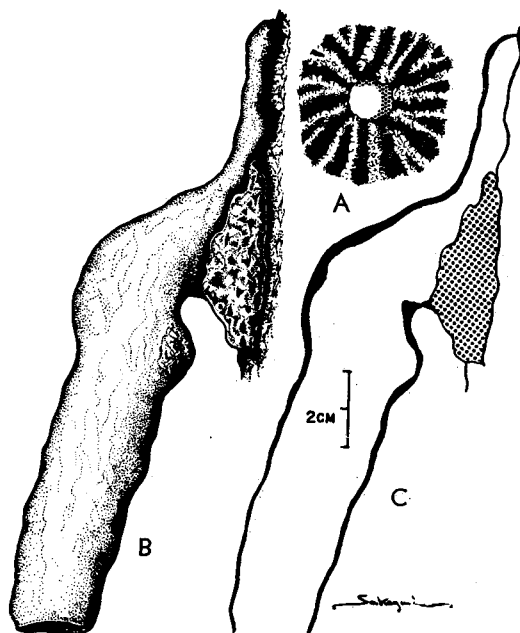


Fig. 4. Nest entrance of *L. ehrhardti* invading the nest of *M. q. quadrifasciata*. A. Incipient stage. Original entrance of *M. q. quadrifasciata* is constricted by addition of cerumen (dotted). B and C. Elongate entrance tube and its longitudinal section. Dotted area means the uncovered entrance architecture by *M. q. quadrifasciata*.

made from white brown soil, hard but rather brittle. But the entrance hole, originally about 10 mm in diameter, had already been constricted to 7 mm by the addition of dark cerumen mixed with finest sand particles (Fig. 4, A, dotted), sharply contrasting with the paler surroundings. Many dead workers of *M. q. quadrifasciata* were scattered on the bottom of the outer hollow.

At the second inspection made on 8 April, 1962, the original entrance architecture by *M. q. quadrifasciata* had already been covered by the dark cerumen, leaving only the lateral parts (Fig. 4, C dotted). An elongated entrance tube resembling the elephant's proboscis had already been constructed. This was taken off and examined in the laboratory. The tube was 11 cm long from the entrance hole at the hollow to the tip, about 3 cm in maximum diameter near the base, and 2 cm in diameter at the tip. The thickness of the tube walls was about 1 mm at the tip, while reaching more than 3 mm near the base. The tube was quite resistant but not brittle, and could still be bent easily. The surface was leather like by a mixture of finest sand particles, but even and provided with no protuberance in contrast to that in *L. limao*. This lack of protuberances is probably characteristic of the species, for again no protuberance was found in the re-built tube taken in the next and final inspection on 16 July, 1962.

Throughout these three inspections it was observed that 1) workers are very mild to the observers, 2) they emit a strong lemon-like odour, and 3) they tend to deposit the waste material below the entrance. All are common to *L. limao* and 1) and 3) to the African congener, *L. cubiceps*.

The nest structure is presented in Fig. 5. The total size was approximately 17 cm in diameter and 16 cm in height. The storage pots were located outside the involucrum, being dark brown, oval or elongate oval and quite large, without structural differentiation of pollen and honey pots. Some measurements were taken as follows (length \times diameter in cm, number of cases in parentheses): 5.0×1.0 (2), 4.0×2.0 (2), 4.0×1.8 (3), 3.0×3.0 (3), 3.0×2.0 (2), 3.0×1.5 (1). The thickness of walls was about 2 mm, but adjacent pots often possessed common walls. Involucrum was dark brown, quite thick, consisting of about 5–8 layers, separated from one another by the interspaces of 3–7 mm, hence about 3 cm in total thickness.

The brood combs were *perfect*, that is, the upper and lower surfaces of each comb were even, without projections of tops and bottoms of cells. Each comb was arranged horizontally, not spirally, connected with one another by means of several pillars of about 1 mm in diameter at the middle, and supported by pillars similar to those within the brood nest cavity. Twelve combs were found in which the 2nd and 3rd (counted from the bottom) were all after the emergence, 5th and 6th were nearly so, and 7th with central empty circle by the emergence, the young immature stages were found only in the first comb, namely, there was only one advancing front (Michener, 1961) and the developmental gradient was concentric. The total height of the brood nest was about 9 cm, the maximum comb diameter

8 cm, and the interspaces between two successive combs 1.5–2.0 mm. The height and diameter of each cell were respectively 6–6.5 mm and 3.5 mm, or, 11 cells per 4 cm. The occurrence or not of the inner tunnel connecting entrance and brood nest was not ascertained.

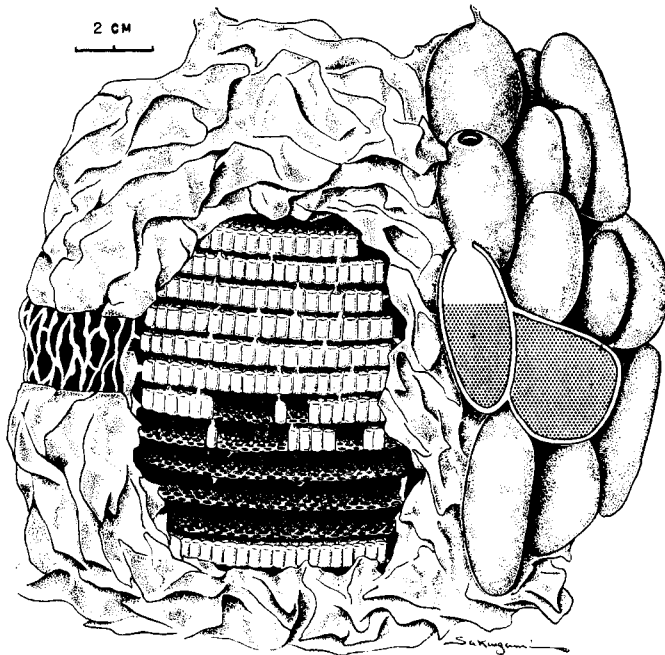


Fig. 5. Nest structure of *L. ehrhardti*. The involucrum is partly removed. A part of involucrum and two honey pots are shown as longitudinal sections.

Summarizing, the nest structure is homologous to that of *L. limao* described by Silvestri, in quite large storage pots, occurrence of involucrum between pots and brood nest and horizontally arranged perfect combs; while it differs from *L. cubiceps* (Araujo, 1958) which possessed clustered brood cells, no involucrum (so far as is known, this seems to be the characteristic common to all cluster-making species and relatively small storage pots after Kerr, person. comm.).

Besides workers and many males, one gravid queen and two virgin ones were found within the nest. Some workers were examined with respect to their ovarian development as published elsewhere (Sakagami *et al.*, 1963). One astonishing fact is that the gravid queen, which was new to science and would be described by Prof. B.L. Lucas de Oliveira, was found *in copula* with one male. One of us (S.F.S.) could not believe this before seeing a sketch made by the other (S.L., Fig. 6, A) and

examining the exposed male reproductive organ (Fig. 6, B). Probably this is the first record of the copulation of gravid queen within the nest in higher insect societies!

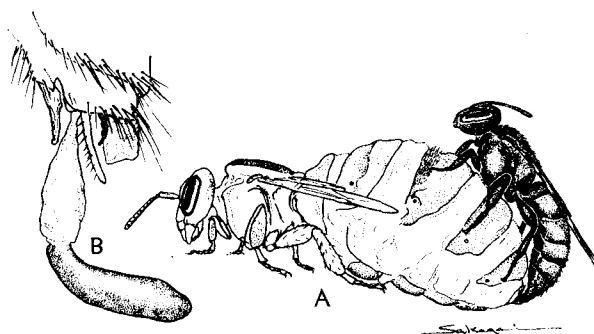


Fig. 6. Copulation of gravid queen and male of *L. ehrhardti*. A. Mating posture, redrawn based upon a field sketch by S. Laroca and dead specimens. B. Exposed genital apparatus of the male in copula.

Kerr and Krauser (1950) observed a queen of *Melipona quadrifasciata quadrifasciata* returning from her nuptial flight and verified that her vagina was filled with the torn off male reproductive organ, including penis and seminal vesicles. Such attachment of male reproduction organs torn off from the owner was seen in a queen of *Nannotrigona (Scaptotrigona) postica* (Latreille) returning from the nuptial flight by one of us (Sakagami & Zucchi, unpub.). Therefore, this seems to be the general mode in stingless bees. In the male of *L. ehrhardti* examined by us, the penis was fully extended and enlarged but still kept intact as seen in the figure, so that it was assumed that the mating act was not perfect. Yet it is remarkable that the mating act was released *within* the nest to the *gravid queen*. This problem can be divided into the two following questions. We cannot give satisfactory answers to both of them, but some comments are given briefly. 1) How was the mating act released within the nest? In both honeybees and stingless bees, it is a rule that the mating is done only outside the nest on the wing. Apparently this must be realized by a number of releasing stimuli. At present we know practically nothing about them, but it is possible that the mating response could be released under the abnormal situation, provided some substituting stimuli, which are different from the adequate ones, but equivalent or nearly so in effect, were given in an appropriate order. For instance, Kerr & Lopez (1962) observed that the flowers of an orchid, *Tirgonidium obtusum* attracted solely the males of *Trigona (Plebeia) droryana* Smith (= *Plebeia (Plebeia)* in Moure, 1961) and these males attempted desperately to mate with flowers (This was later repeatedly confirmed by one of us (S.F.S.) in Rio Claro, S.P.). In this case, obviously, some

factors in the flowers, probably a specific odour, acted as a substituting stimulus to release the mating act. 2) How did the male succeed in inserting his penis in the queen's vagina?. The release of the mating response to the gravid queen is not difficult to assume. One of us (S.F.S.) observed that the males of *Nannotrigona* (*Scaptotrigona*) *postica* swarming in front of the nests eagerly attempted to copulate with a gravid queen offered experimentally, but none of them could take the normal copulation posture (Sakagami & Zucchi, unpub.). To insert the penis in the queen's vagina, the male must grasp some parts of the queen's body to set himself firmly on the latter. This is very difficult in the case of a gravid queen. Because of the enormous bulk of her metasoma the forelegs of the male cannot reach her mesosoma, and the metasoma itself has few structures to be grasped by the male. The only possible interpretation is that the male could pose by fixing his fore-legs on the third metasomal tergum of the queen, which had anteriorly a patch of dense, rather stout hairs (Fig. 6, A).

III. Some problems to be solved by further studies

There are still many problems to be solved by further studies as to the bionomics of this singular group. It would be convenient to add here brief comments upon some of them, in order to call them to the attention of other research workers.

1) *Obligatory cleptobiosis or not?* This seems to be nearly solved. But we must still keep in mind the criticism by Schwarz cited in the introduction, for his opinions are themselves logically appropriate. The frequent records on the poisonous honey of *L. limao* must have some concealed causes to be clarified. Further, it may be interesting to know whether or not *Lestrimelitta* cannot forage by themselves even by the application of training methods.

2) *Variability in entrance architecture:* In the present paper, the two major trends in the entrance architecture were cited. But we still do not know why one of them prevails under particular conditions. Whether or not such trends geographically determined, and, if the latter is the case, what factor affects the development of a definite pattern in each colony?

3) *Frequency of invasion of nests of other stingless bees:* The present work revealed the frequent occurrence of the invasion by *Lestrimelitta* of the nest of other stingless bee species. But so far as we are aware, nobody has presented the question about its frequency. Whether or not such invasion is obligatory? If facultative, how frequently does it occur and what role does it play in the life cycle of this group?

4) *Lestrimelitta* attacks diverse stingless bee species, but there seems to occur some preference of victim in each locality, such as *Plebeia emerina* in Curitiba and *Nannotrigona testaceicornis* in Panama Canal Zone (Michener, 1946). Obviously, such preference may vary from place to place, depending on the make-up of stingless bee fauna. If such local preference within the distribution range

would be studied, we could have some ideas on the characteristics common to the species preferred by them, or those species not attacked or to those attacked but which can defend themselves effectively. It is also interesting to know whether or not the peculiar odour of *Lestrimelitta* affects different species differently.

5) In the present paper, it was recorded that *L. limao* attacked one particular colony of *Plebeia emerina* at regular intervals. This event leads us to a very fascinating problem: *Structure of their hunting range*, including diverse questions as follows: A) What structure has their hunting range? Its extent in relation to the colony size and density of victim colonies. Flight range and minimum density of victim colonies to support the survival etc. B) Do they visit their *properties* without particular order or do they make regular rotation? C) Do they issue several robbing parties, each procuring a different victim colony at one and the same time, or do they concentrate their efforts on one particular colony at a given time? D) Is the issue of robbing parties performed continuously or with some periodicity? In other words, do they issue the robbing party only after the consumption of the booty by the last one?

6) *Communication system in Lestrimelitta*: The work of Lindauer and Kerr (1958) showed the occurrence of an efficient communication system in some Neotropical stingless bees. But in both honeybees and stingless bees, the natural food exists as small, rather poor sources scatter over a vast area. The concentrated and rich sources such as in experimental situation, in which the communication has been studied, are rather an exceptional luxury to them. On the other hand, such concentrated sources may be a rule in the life of *Lestrimelitta* because of its peculiar mode of life. It is highly probable that this group possesses an advanced communication system in connection with such special distribution of their food.

7) Because of an extreme morphological differentiation, probably partly due to the secondary modification, it is difficult to trace the phyletic relation between *Lestrimelitta* and the other stingless bees, as shown in a pessimism by Schwarz (1948). In such cases, we must seek further evidence not only in morphology but also in behaviour characteristics. The precise studies of behaviour characteristics, especially of the elementary motor-response patterns might enlighten this difficult problem.

Summary

Some additional observations were made as to the habits of cleptobiotic stingless bees, the genus *Lestrimelitta* Friese, which are summarized as follows:

1) *L. limao* (Smith) seems frequently to usurp the nest of *Melipona quadrifasciata* Lepeletier. Two instances were recorded.

2) A highly complicated nest architecture of *L. limao* was recorded, in which both principal features of the entrance architecture so far recorded in this species, production of surplus protuberances and elongation of main tube, were found in combination.

3) A continuous observation of the repair and development of entrance architecture showed a relatively poor integration of independent contributions by each worker to the whole pattern. Some considerations were given as to the related phenomena in insect societies.

4) Behaviour of *L. limao* at the entrance was observed, including a) mutual mimetic reaction in returning bees, b) influence of air temperature and insolation upon the flight activities, c) fanning behaviour, d) mild disposition of guard bees even to the robbing workers of *Plebeia* (*Plebeia*) *emerina* Friese. The last observation is interesting, because *P. emerina* is the principal victim of *L. limao* in Curitiba.

5) A probably unsuccessful invasion of *L. limao* of a nest of *P. emerina* was closely described, together with some interpretation of the intermittent occupations of the nest entrance by *L. limao*.

6) A brief note was added concerning the robbing behaviour of *L. limao* in Curitiba, based upon the information offered by Prof. Lucas de Oliveira.

7) The very rare species, *L. ehrhardti*, was discovered when this invaded the nest of *Melipona quadrifasciata quadrifasciata*. This species is similar to *L. limao* in its mild disposition, strong lemon-like odour and accumulation of waste material immediately below the nest entrance.

8) The description of the nest of *L. ehrhardti* was given. It was homologous to that of *L. limao* in quite large storage pots, perfect combs arranged horizontally and occurrence of involucrum between brood nest and storage pots, while different in the lack of protuberances in the entrance architecture.

9) An unusual event, the copulation of the gravid queen of *L. ehrhardti* was recorded within the nest together with some related comments.

10) Some still unsolved problems as to the bionomics of *Lestrimelitta* were enumerated, expecting their clarification in future.

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