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COMPARATIVE STUDY OF *CORPORA ALATA* IN BRAZILIAN STINGLESS BEES [1]

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ABSTRACT

1. A comparative study of *corpora alata* in thirty-two species of stingless bees and two subspecies of honeybees has been made in the fields of biometry (size, number of nuclei, volume) and of histology (quantity of chromatin, staining affinity, vacuolization).

2. These are found to be common characters within each subgenus, while considerable differences are found among them. In general *Apis*, the *Frieseomelitta* and *Partamona*- groups show positive qualities, probably indicating secretory activity; the *Scaptotrigona*- group occupies an intermediate position; and the *Melipona*- and the *Trigona*- groups show extremely low or negative characters.

The correlation between activities of *corpora alata* and the states of worker ovary development found for the same species in a previous report, are discussed.

There are many publications concerning Hymenopteran *corpora alata*, including anatomical descriptions, biometrical studies, and studies of endocrinological interaction with other organs, especially with the reprodutive system, or the development of worker ovaries (Hanström, 1839; Nabert, 1913; Palm, 1948; Williams, 1958, etc.). According to our studies, on the other hand, it has been verified that among colonies of the so-called stingless bees three types of development of worker ovaries exist under normal queen-right condition, e.g., 1st. type having well-developed worker ovaries, e.g. *Trigona (Scaptotrigona) postica*, *Melipona*-group, and others; 2nd. type in which worker ovaries never develop, e. g., *Frieseomelitta*-group, *Hypotrigona müllerii, Duckeola ghilianii, Par-*

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tamona-group, and others; 3rd. type having partially developed workers ovaries, e. g., *Trigona (Plebeia) droryana, Trigona (Nannotrigona) testaceicornis.* (Sakagami & *al.,* 1963).

The present study has been carried out with the aim, of making biometrical and histological comparisons of *corpora alata* among two tribes of stingless bee *(Trigonini* and *Meliponini)* and *Apis,* attempting to decide the interrelations between activities of the *corpora alata* and development of worker ovaries, to contribute to the main objective of our bee investigators, which is the understanding of the evolution of social bees.

Materials and methods

The materials for this investigation consisted of five pairs of *corpora alata* of worker bees, principally foragers, per species, or of ten *corpora alata,* when a pair could not be obtained.

Fifteen species were collected during the expedition to Manaus, Amazonas, and the other seventeen were reared in our laboratory in natural nests collected at various localities. One Ethiopian species and two subspecies of the honey bee were included in this study.

The species studied were the following (the abbreviations listed for each species, are the ones used in the text):

Trigona (Cephalotrigona) femorata Smith	Manaus, Am	CF
T. (T.) cilipes cilipes (Fabricius)	Manaus, Am	TCC
T. (T.) crassipes (Fabricius)	Manaus, Am	TCR
T. (T.) hyalinata bruneri Cockerell	Manaus, Am	THB
T. (T.) spinipes (Fabricius)	Rio Claro, SP	TS
T. (Tetragona) dorsalis Smith	Manaus, Am	TDo
T. (Frieseomelitta) flavicornis (Fabricius)	Manaus, Am	TFl
T. (F.) freiremaiai (Moure)	Guarapari, SP	TF
T. (F.) varia geneoscantha Moure	Manaus, Am	TVG
T. (Duckeola) ghilianii (Spinola)	Manaus, Am	TG
T. (Tetragonisca) jaty Smith	Rio Claro, SP	TJ
T. (Ptilotrigona) lurida Smith	Manaus, Am	TL
T. (Plebeia) droryana Friese	Rio Claro, SP	TD
T. (Friesella) schrottkyi Friese	Rio Claro, SP	TSc
T. (Partamona) cupira Smith	Rio Claro, SP	TC
T. (P.) nigrior (Cockerell)	Cristalina, Go	TN
T. (P.) pearsoni (Schwartz)	Cristalina, Go	TPe
T. (P.) testacea testacea Cockerell	Manaus, Am	TTT
T. (Nannotrigona) testaceicornis (Lepeletier)	Rio Claro, SP	TT
T. (Scaptotrigona) bipunctata (Lepeletier)	Rio Claro, SP	TB

T. (S.) postica Latreille	Piracicaba, SP	TP
T. (S.) xanthotricha (Moure)	Cabreuva, SP	TX
Scaura (Scaura) tenuis (Ducke)	Manaus, Am	ST
Meliponula bocandei (Spinola)	Luanda, Angola	MB
Melipona compressipes manaosensis Schwartz	Manaus, Am	MCM
M. marginata amazonica Schulz	Manaus, Am	MMA
M. marginata marginata Lepeletier	Manaus, Am	MMM
M. pseudocentris pseudocentris Cockerell	Manaus, Am	MPP
M. quadrifasciata anthidioides Lepeletier	Rio Claro, SP	MQA
M. quinquefasciata Lepeletier	Cristalina, Go	MQ
M. seminigra merrillae Cockerell	Manaus, Am	MSM
Apis mellifera adansonii Latreille	Johanesburg.	AMA
A. mellifera ligustica Spinola	Imported from USA.	AML

The fresh heads were submerged and dissected in a 1% Ringer's solution and the brains with *corpora alata* were immediately transferred to Bouin's fixative. The materials obtained during the expedition were fixed in Kahle's solution, and the dissected brains were also refixed in Bouin's solution. They were cut sagitally into 7 micra thick sections and stained with Delafield's haematoxylin and eosin. The volumes of *corpora alata* were calculated by the following formula:

$$V = \frac{7 \pi \sum_{1}^{n} (A_i \, . \, B_i)}{4}$$

A and B, the longest and shortest diameters, in micra, of *corpora alata* presented in each serial section respectivelly.

n, number of serial sections of each *corpus alatum*

V, volume in cubic micra.

The *corpora alata* are spherical or ellipsoid in general, therefore, the sections show the forms of a circle or oval. But when the *corpora alata* are flattened in an extremely elongated elipsoid, or into irregular ellipsoids, the formula above used does not give exact value, and in these cases we applied it only for approximate comparison.

The nuclei in each section of *corpora alata* were counted under oil immersion; the total number was obtained by summing all sections, but when one nucleus appeared in two sections, for example, we discounted one from the total number.

We found that the nuclei of *corpora alata* may be divided into two types of different sizes. We estimated the percentage of large nuclei (%) based in the series of *corpora alata* for each species; we calculated the mean cell volume (c. v.) appertaining to each nucleus by dividing the total volume by the total number of nuclei. To relate the volume of *corpora alata* to the size of insect we measured the width of the thorax (in mm; distance between the bases of both wings) and divided the mean volume by the cube of this distance. The quantity so obtained corresponds to V. I. in table 1.

Results

General remarks

The *corpus alatum* has a spherical or more or less elongated shape, and is situated on the dorso-lateral side of the oesophagus. It is connected with the *corpora cardiaca,* which lay dorsally on the oesophagus. The connections are at the posterior ends of the *corpora alata,* and therefore sometimes sections of *corpora alata* appear completely isolated from the *corpora cardiaca.* The *corpora alata* are covered by a very thin epithelial membrane which has degenerate nuclei. The *corpora alata* contain fairly large cells of variable size, with the cell-boundaries polygonal and usually distinctly observable. The nucleus contains several small nucleoli and the nucleoplasm is generally very clear, not rich in chromatin; but a degenerating nucleus has an irregular shape and shows strong affinity for haematoxylin. When the *corpora alata* are extremely flattened, nuclei are also flattened and very rich in chromatin. The nuclei are distributed uniformly in the *corpora alata,* but sometimes they concentrate superficially or radialy. The cytoplasm is finely granular or fibrillar; sometimes it shows vacuoles of various sizes, especially in certain of the examined species.

Though both *corpora alata* and *corpora cardiaca* are paired organs, we found an unpaired *corpus alatum* quite frequently in the sections. As we show later this phenomena seems to be due to a degeneration in the course of worker bee life.

Biometrical observation

The results are shown in table 1, in which the following data are shown for each species: total number of nuclei in each *corpus alatum* (N); number of large nuclei (N'); maximal width of serial sections (W); maximal height (H); maximal antero-posterior distance (D); volume of each *corpus alatum* (V, x 100 μ^3); serial number of the insect (P), indicating also the pairing or non-pairing of the *corpora alata* and the number of insects used; the mean value (X); percentage of large nuclei (%); cell volume (C. V.); and volume index (V. I.).

From the table we find the following:

1) In both N and V relatively large variations are observed throughout the species examined; especially in *T. cillipes cillipes; T. crassipes; T. hyalinata bruneri; T. spinipes; T. (Frieseomelitta) flavicornis; T. (F.) varia geneoscantha; T. (Tetragonisca) jaty;*

Meliponula bocandei; T. (Friesella) schrottkyi; T. (Partamona) cupira; T. (P.) nigrior; T. (P.) pearsoni; T. (Nannotrigona) testaceicornis; T. (Scaptotrigona) bipuntacta; T. (S.) postica; T. (S.) xanthotricha; M. pseudocentris pseudocentris; M. quadrifasciata anthidioides; Apis mellifera adansonii (queen); *Apis mellifera ligustica* (queen and worker) the minimum volume of one *corpus alatum* was less than half of that of the maximum. Materials were obtained from the worker bees, and these variations may be related to the age of the worker in addition to individual variations.

2) Where N' is the greater it might be suggested that the secretory activity of the *corpora alata* is more marked. Though N' shows also comparatively great variation in the same species, the following species give more than 30% of (%): *T. (Frieseomelitta) flavicornis; Scaura (Scaura) tenuis; T. (Partamona) cupira; T. (P.) nigrior; T. (P.) pearsoni; T. (P.) testacea testacea; Apis mellifera adansonii* (queen); *Apis mellifera ligustica* (worker). On the other hand, in *T. spinipes; Meliponula bocandei; M. marginata amazonica; M. quinquefasciata,* they are less than 10%, indicating a generally lesser development in *Melipona.*

3) Cell volume appears to be correlated to the body size in the stingless bees, a group of small body size, *Scaura (Scaura) tenuis; T. (Friesella) schrottkyi; T. (Tetragona) dorsalis; T. crassipes,* shows the average value less than 3 μ^3 per nucleus; however, in a group of large body size *T. (Cephalotrigona) femorata; T. (Duckeola) ghilianii; Meliponula bocandei; M. compressipes manaosensis* and *M. seminigra merrillae)* it is more than 5 μ^3. But it is notable that some species not having such large body size show also great cell volume, of more than 5 μ^3: *T. (Frieseomelitta) flavicornis; T. (F.) freiremaiai; T. (Partamona) cupira; T. (P.) nigrior; T. (P.) pearsoni T. (Scaptotrigona) postica;* and *T. (S.) xanthotricha.* On the other hand the *Melipona*-group, which has relatively large body size, shows small values, less than 3 μ^3: *M. marginata amazonica; M. marginata marginata; M. pseudocentris pseudocentris; M. quadrifasciata anthidioides* and *M. quinquefasciata.* In the honey bee, the cell volume is extremely large when compared to that in stingless bees.

4) V. I. indicates a correlation between volume of *corpora allata* and body size; when the former is comparatively large, V. I. becomes larger. In the following species V. I. is less than 50: *T.* (*Cephalotrigona*) *femorata; T. cilipes cilipes; T. crassipes; T. hyalinata bruneri; T. spinipes; T. (Ptilotrigona) lurida; Meliponula bocandei T. (Partamona) pearsoni; T. Nannotrigona) testaceicornis; T.* (*Scaptotrigona*) *bipunctata; T.* (*S.*) *postica; M. compressipes manaosensis; M. marginata amazonica; M. marginata marginata; M. pseudocentris pseudocentris; M. quadrifasciata anthidioides; M. quinquefasciata* and *M. seminigramerrillae.* The following species show V. I. more than 100: *T.* (*Frieseomelitta*) *flavicornis; T. (F.) freiremaiai; T. (Tetragonisca) jaty; Apis mellifera adansonii* (queen) and *Apis mellifera ligustica* (worker). Among them all *T. (Frieseomelitta) flavicornis* and *T. (F.) freiremaiai,* have specially large values and *M. pseudocentris pseudocentris* shows the minimum value.

If we compare queen and worker of the two honey bee subspecies, a curious relation is found. The queen of *Apis mellifera adansonii* has a larger mean V. and V. I. than the worker, but in *Apis mellifera ligustica* the queen shows a lesser mean V. and V. I. than the worker.

5) The column P indicates the individual bee and brain examined and the presence of paired *corpora alata.* As mentioned above, sometimes *corpora alata* were not paired. For example, in *T. (Cephalotrigona) femorata,* 10 *corpora alata* were observed; the first 4 were paired and obtained from 2 brains, while the remaining 6 were singular; in total we use 8 brains for 10 *corpora alata.* When only one *corpus alatum* was present, it very frequently perfect, as were the paired *corpora cardiaca.* Therefore it is unlikely that the missing *corpus alatum* had been lost due to dissection or in the process of microtechnique. We dissected and cut more than 10 brains in each species, excepting those collected in Manaus, of which the available number was sometimes small. The ratio of normal (paired) to degenerated (unpaired) shown in table 2 does not mean much because of the smallness of the samples, but it does suggest an outline of the degeneration tendency in each species for which more than 7 brains were necessary, as follows: *T. (Cephalotrigona) femorata; T. crassipes; T. (Duckeola) ghilianii; T. (Partamona) cupira; T. (P.) nigrior; T. (Scaptotrigona) postica; T. (S.) xanthotricha; M. pseudocentris pseudocentris* and *M. quadrifasciata anthidioides.* The *Partamona* group shows a strong tendency to degeneration; in the *Melipona* group, *M. pseudocentris pseudocentris* and *M. quadrifasciata anthidioides* show a strong tendency than the others.

Histological observations

In figures 1-72 transverse sections of *corpora alata* are shown, all photographs being to the same enlargement (x 140) for convenient comparison. Often the maximal sections of the two *corpora alata* dit not occur in the same cut; in these cases the maximal left and right sections were mounted jointly; the two sides are always from the same brain. (Ex. Fig. 3-TCC, Fig. 5 TCr; Fig. 9-TS; Fig. 15-TF; Fig. 23-TL; Fig. 29-TD; Fig. 33-TC; Fig. 45-TP; Fig. 47-TX; Fig. 49-MCM; Fig. 53-MMM; Fig. 57-MQA and Fig. 61-MSM).

With respect to the histological analysis, the following characters might be related to the functioning of the *corpora alata:*

a) the size of the nucleus and its degenerating figure,
b) quantity of chromatin and its distribution,
c) cell boundary,
d) the staining affinity of cytoplasm, and
e) vacuolization of cytoplasm.

We will now describe these characters in each species, excepting the size of nucleus which has already been noted.

Trigona (Cephalotrigona) femorata

Both *corpora alata* and the large nuclei are flattened; often the nuclei show polygonal forms, varying from 11 to 13 μ in size.

Nuclei are strongly stained and very rich in chromatin. Cell boundaries are not clear, staining affinity of cytoplasm is weak, and vacuoles rarely appear.

Trigona cilipes cilipes

Corpora alata are very flattened and irregular in form. Large nuclei are also elongated and very rich in chromatin and small degenerating ones stain very darkly. The several nucleoli in large nuclei are mixed with much fine chromatin. Cell boundaries are obscure and no vacuoles exist.

Trigona crassipes

Corpora alata are flattened, more or less rich in chromatin and are distributed uniformly in the nucleoplasm; 2 to 3, sometimes 4 to 5 nucleoli in the oval nuclei, the number is generally higher when the nuclei are small. The large nuclei generally 5 x 7 μ and the small less than 4 μ. Cytoplasm stains weakly and cell boundaries and vacuoles are lacking.

Trigona hyalinata bruneri

Corpora alata are flattened. In the large nuclei remarkably numerous and measuring 6 to 8 μ in diameter, chromatin is very abundant. No cell boundaries and vacuoles are apparent.

Trigona spinipes

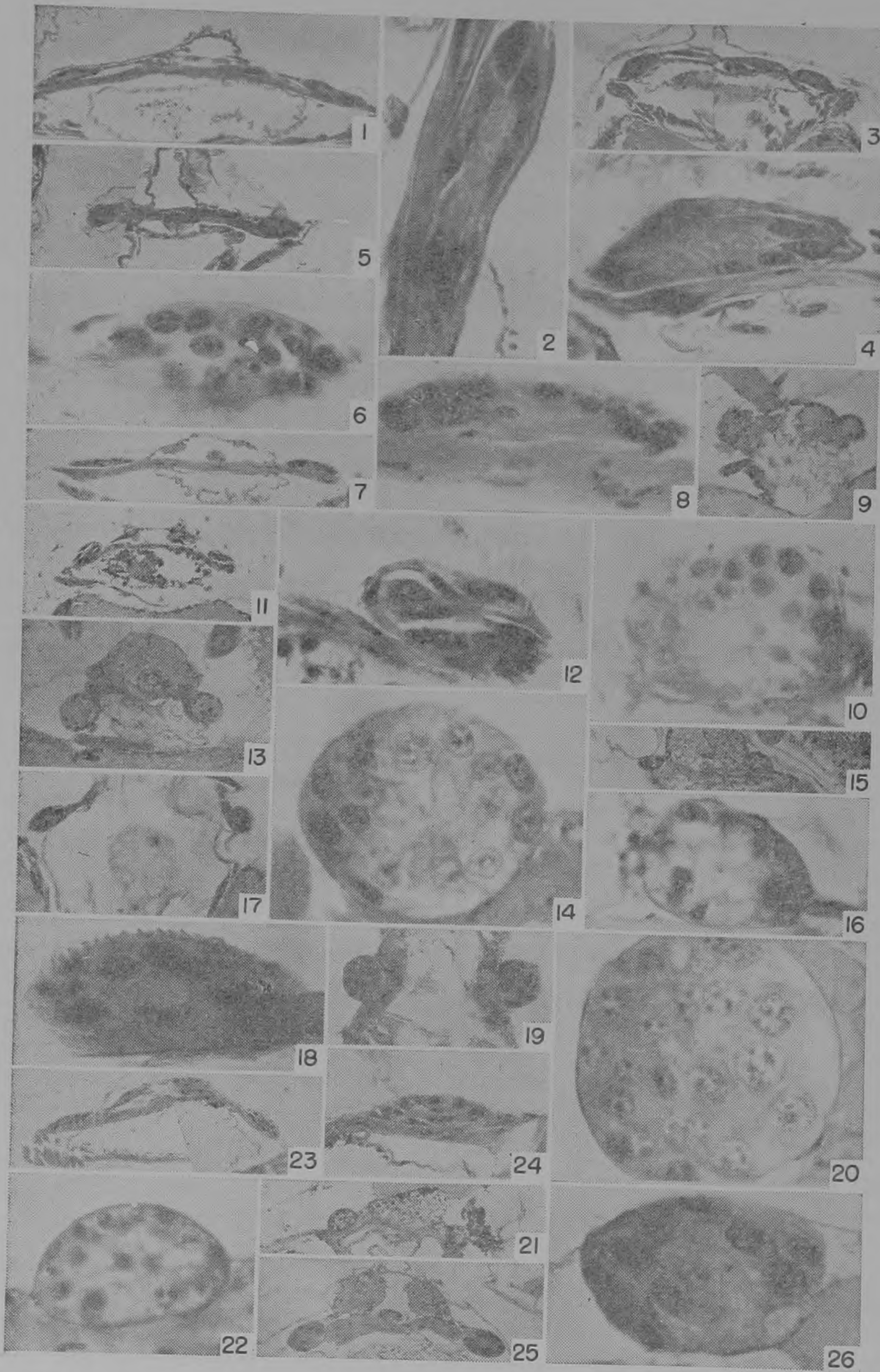
Corpora alata are oval. The nuclei vary extremely in size, large ones amount to 7 x 9 μ in oval form while the small ones are 2. 5 μ in diameter. Chromatin is rather less and well scattered in the clear nucleoplasm. Cell boundaries are indistinct, and several large vacuoles are contained in the cytoplasm, of which the staining affinity is very weak.

Trigona (Tetragona) dorsalis

Corpora alata are oval, but nuclei are slightly elongated measuring 9 to 11 μ in the longer axis. Large nuclei in high proportion. Much chromatin and several nucleoli contained inside the large nucleus. A few vacuoles appear in rare cases while the cytoplasm has no cell boundaries.

Trigona (Frieseomelitta) flavicornis

Corpora alata are almost spherical and oval; quite large nuclei, 7 x 9 μ in diameter, are extremely numerous. Their nucleoplasm



Transversal section of *corpora alata*. 1-2: *Trigona femorata;* 3-4: *Trigona cilipes cilipes;* 5-6: *Trigona crassipes;* 7-8: *Trigona hyalina bruneri*; 9-10: *Trigona spinipes;* 11-12: *Trigona dorsalis;* 13-14: *Trigona flavicornis;* 15-16: *Trigona freiremaiai;* 17-18: *Trigona varia geneoscantha;* 19-20: *Trigona ghilianii;* 21-22: *Trigona jaty;* 23-24: *Trigona lurida*; 25-26: *Meliponula bocandei*. Figures 1, 3, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23 and 25 in same scale (x 140); Figures 2, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24 and 26 in oil immersion (x 880).

is clear, somewhat poor in chromatin and include 2 or 3 nucleoli. The small nuclei are irregular and more or less rich in chromatin. Vacuolization proceeds strongly around the large nucleus and the cell boundaries are distinct. Staining affinity of the cytoplasm is weak.

Trigona (Frieseomelitta) freiremaiai

Oval *corpora alata* were always found paired in the sections, but histological characters were varied: i. e., some large nuclei measuring 7 to 9 μ in diameter, are rich in both nucleoli and chromatin vacuolization is remarkable, cytoplasm hardly stains with eosin, and cell boundaries are quite clear; but others have contrary or negative features. The small nuclei tend to be irregular in their pycnosis.

Trigona (Frieseomelitta) varia geneoscantha

Corpora alata are almost flattened; large nucleus, with a few nucleoli, is rich in chromatin, varying 7 to 9 μ in diameter, while the small 3 to 5 μ. Vacuolization does not occur and cell boundaries are obscure. Proportion of large nuclei is relatively high.

Trigona (Duckeola) ghilianii

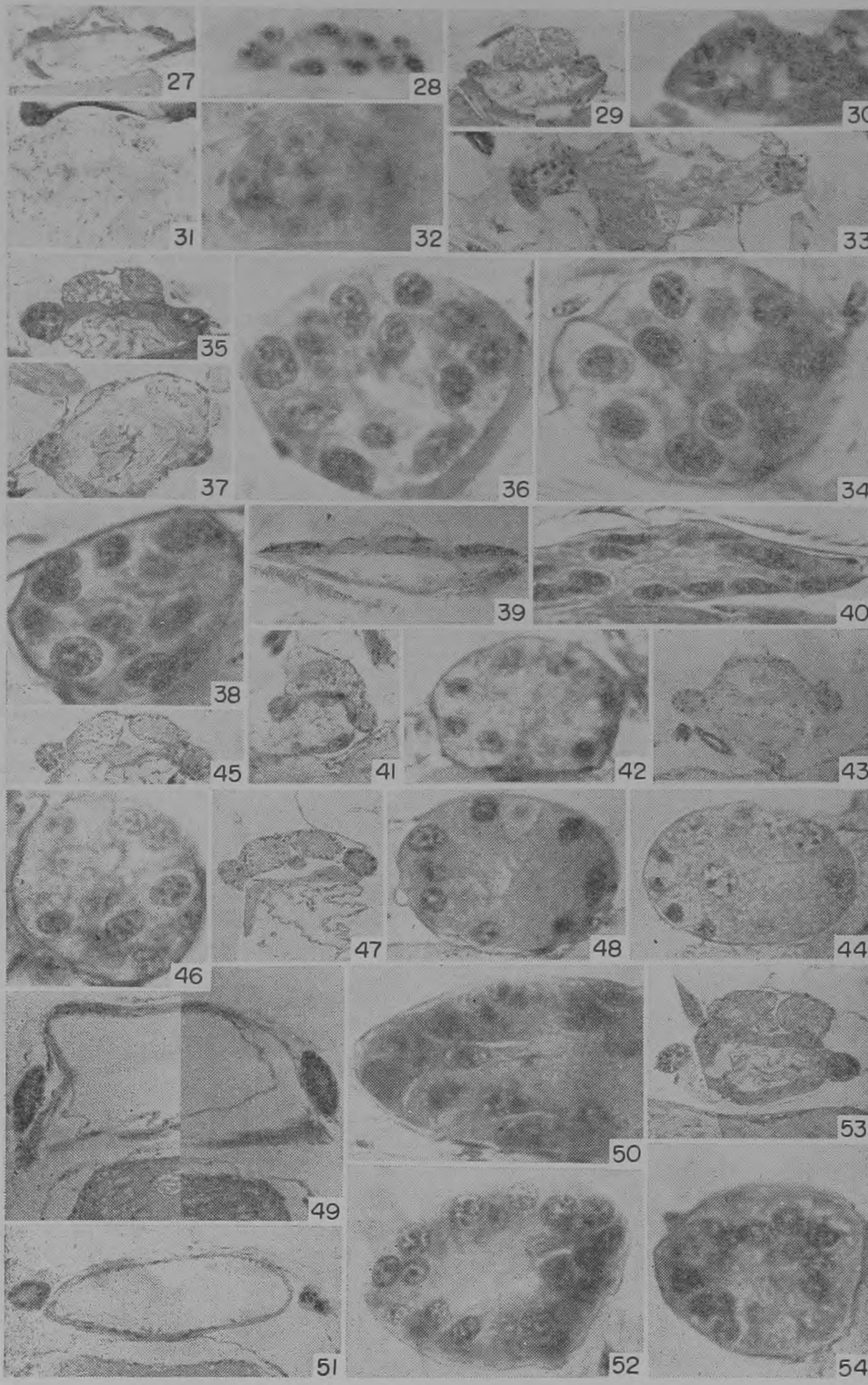
Corpora alata are spherical. Large nuclei about 9 μ in diameter, 2 to 3 well spaced nucleoli. The nucleoplasm is clear and not rich in chromatin. Small nuclei are slightly irregular in shape and have pycnotic figures. Vacuolization varies, some have much around the nucleus, while the others do not. Cell boundaries are not always distinct, and the cytoplasm shows moderate affinity to stain.

Trigona (Tetragonisca) jaty

Corpora alata are oval and histological characters rather positive. Two to four large nucleoli and a considerable amount of chromatin; small vacuoles recognisable around the nuclei. The large nuclei vary in size 7 to 9 μ in diameter. Cell boundaries are quite distinct. But irregular, pycnotic, small nuclei are found scattered among the large nuclei.

Trigona (Ptilotrigona) lurida

Corpora alata and nuclei are flattened. The latter vary in size 7 to 9 μ in diameter. Nuclei stain strongly with haematoxilin and the small ones show completely pycnotic figures. There are no vacuoles, and the cell boundaries are obscure.



Transversal section of *corpora alata*. 27-28: *Scaura tenuis;* 29-30: *Trigona droryana;* 31-32: *Trigona schrottkyi;* 33-34: *Trigona cupira;* 35-36: *Trigona nigrior;* 37-38: *Trigona pearsonii*; 39-40: *Trigona testacea testacea;* 41-42: *Trigona testaceicornis;* 43-44: *Trigona bipunctata;* 45-46: *Trigona postica;* 47-48: *Trigona xanthotricha;* 49-50: *Melipona compressipes manaosensis;* 51-52: *Melipona marginata amazonica;* 53-54: *Melipona marginata marginata.* Figures 27, 29, 31, 33, 35, 37, 39, 41, 43, 45, 47, 49, 51, and 53 in same scale (x 140); Figures 28, 30, 32, 34, 36, 38, 40, 42, 44, 46, 48, 50, 52 and 54 in oil immersion (x 880).

Scaura (Scaura) tenuis

Though samples are small, large nuclei are in high proportion and rich in chromatin. No vacuoles and cell boundaries indistinct.

Trigona (Plebeia) droryana

Corpora alata are small but round. Nuclei are comparatively clear, measuring about 6 μ in diameter, and excepting the small ones are irregular and dark stained. A high proportion of large nuclei is seen. Affinity of cytoplasm for basophile stain is strong; the cell boundaries are distinct, and vacuolization appears frequently around the nuclei.

Trigona (Friesella) schrottkyi

Corpora alata are oval, chromatin is more or less poor in the nuclei, which vary 4 to 7 μ in diameter. Vacuolization is rarely found. Cell boundaries are generally obscure but a few show them distinctly. Staining affinity of the cytoplasm is weak.

Trigona (Partamona) cupira

Corpora alata are spherical. Large oval nuclei are in high proportion, measuring 9 to 12 μ in diameter. A few large nucleoli are distributed in each; chromatin is abundant. In regard to cell boundaries and vacuolization great variations are seen. Some (about half number examined) have positive characters, while the others are quite negative, these states being independent of the presence of chromatin. Vacuoles are always found surrounding the nuclei; the cytoplasm stains weakly with eosin.

Trigona (Partamona) nigrior

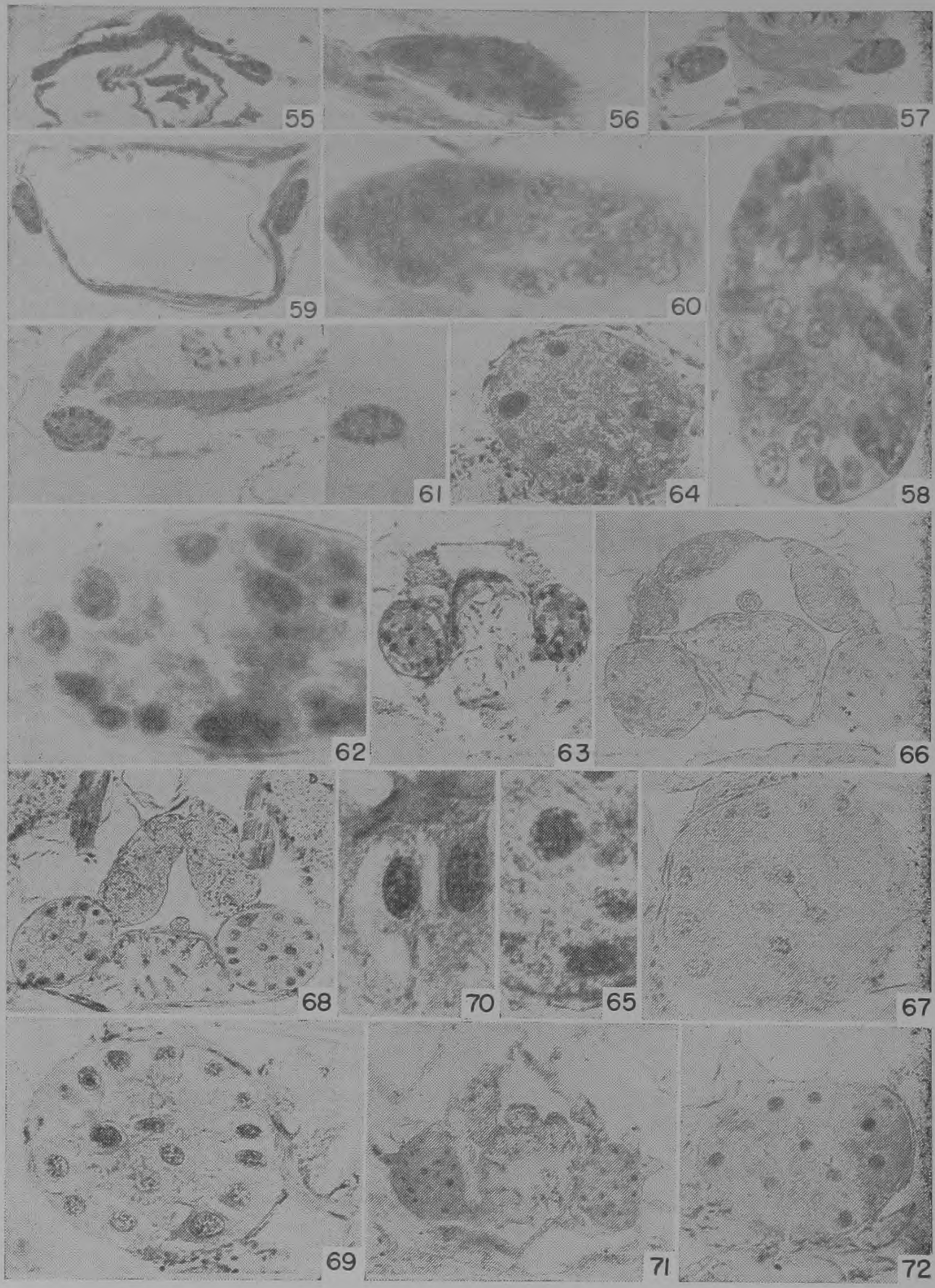
The characters are quite similar to those of *T. (Partamona) cupira* above, but vacuolization proceeds more strongly and the amount of chromatin is relatively small.

Trigona (Partamona) pearsoni

Corpora alata are oval and again there are similarities with *T. (P.) cupira.* A remarkable high proportion of large nuclei is seen, measuring 10 to 12 μ; vacuolization is very variable but the cell boundaries are always distinct.

Trigona (Partamona) testacea testacea

Corpora alata and nuclei are very flattened. Large nuclei are seen in high percentage, measuring 9 to 11 μ in long axis, in these



Transversal section of *corpora alata*. 55-56: *Melipona pseudocentris pseudocentris;* 57-58: *Melipona quadrifasciata anthidioides*; 59-60: *Melipona quinquefasciata;* 61-62: *Melipona seminigra merrillae;* 63-65: *Apis mellifera adansonii*, worker; 66-67: *Apis mellifera adansonii*, queen, 68-70: *Apis mellifera ligustica*, worker; 71-72: *Apis mellifera ligustica*, queen. Figures 55, 57, 59, 61, 63, 66, 68 and 71 in same scale (x 140); Figures 64, 67, 69 and 72 in oil immersion (x 350); Figures 56, 58, 60, 62, 65, and 70 in oil immersion (x 880).

dark and rich chromatin is contained; the small ones are irregular and crushed, or polygonal. Cell boundaries are obscure and vacuoles often appear.

Trigona (Nannotrigona) testaceicornis

Corpora alata are oval. The small nuclei are stained dark and irregular, showing pycnosis, while the large ones have a few nucleoli in the center. Chromatin not rich. Cell boundaries fairly distinct. A round the large nuclei a small degree of vacuolization occurs.

Trigona (Scaptotrigona) bipunctata

Corpora alata are oval. The large oval nuclei measuring 6 x 8 μ, are clear, not rich in chromatin and some have 2 to 3 nucleoli. Cell boundaries are relatively distinct and vacuolization proceeds actively the nuclei.

Trigona (Scaptotrigona) postica

Corpora alata are quite spherical, and the large nuclei vary from 7 to 9 μ in diameter. A few nucleoli are visible while chromatin is poor. In some cases cell boundaries are distinct and less vacuoles exist in the cytoplasm; but cells of opposite character occur. The nuclei tend to concentrate near the surface of the corpora alata. The small nuclei are irregular and dark stained.

Trigona (Partamona) xanthotricha

Corpora alata are oval. The large nuclei measuring from 6 to 8 μ in diameter, are concentrated near the surface of the *corpora alata,* and are not rich in chromatin. Generally vacuolization takes place actively at the periphery of the nuclei, sometimes one of the vacuoles becomes very large, about 15 μ in diameter; but cell boundaries are distinct. The small nuclei are irregular in shape and dark stained, measuring 2 to 3 μ.

Meliponula bocandei

Corpora alata are oval, with large nuclei measuring 6 x 9 μ. Often the nuclei are elongated. They are rich in chromatin, have 2 to 4 nucleoli; small nuclei are darkly stained and show pycnotic figures. Active and large vacuoles are seen in the cytoplasm in a proportion; they measure 8 x 12 μ. Cytoplasm is basophile, and the cell boundaries are fairly clear.

Melipona compressipes manaosensis

Corpora alata are slightly elongated. The large nuclei contain a few nucleoli and a great amount of chromatin; they measure about 11 μ in diameter. Vacuolization proceeds actively around the nuclei. Cell boundaries are quite obscure. Cytoplasm stains strongly with eosin.

Melipona marginata amazonica

Corpora alata are oval. The nuclei vary from 7 to 9 μ in diameter, are very rich in chromatin and distributed peripherally. Occurrence of vacuoles is rare and the cell boundaries are indistinct.

Melipona marginata marginata

Corpora alata are oval. The large nuclei are more or less rich in chromatin, measuring from 7 to 9 μ in diameter, but they are scarce; the small ones are irregular in form, about 5 μ, with dark centres. Vacuolization takes place strongly around the nucleus. Cytoplasm stains weakly and cell boundaries are indistinct.

Melipona pseudocentris pseudocentris

Corpora alata are very flattened; the nuclei have a large amount of chromatin and are strongly stained. They vary in size from 7 to 9 μ in diameter. Vacuolization is weak and the cell boundaries obscure.

Melipona quadrifasciata anthidioides

Corpora alata are oval. The large nuclei measure 9 to 11 μ in diameter, are not rich in chromatin, and are distributed near the surface of the corpora alata. The small nuclei are sometimes arranged radially. They measure about 4 μ, and are irregularly dark. Cell boundaries are obscure, and vacuolization appears frequently.

Melipona quinquefasciata

Corpora alata are elongated. The large nuclei have rather clear nucleoplasm, poor in chromatin. They are oval, about 8 x 11 μ and contain one or two nucleoli. Often their long axes are arranged parallel to that of the *corpus alatum*. The small ones occur in great numbers, are irregular and darkly stained, measuring 3 μ in diameter. No vacuolization takes place and the cell boundaries are indisctinct.

Melipona seminigra merrillae

Corpora alata are somewhat elongated. The round nuclei, both the large and the small, are rich in chromatin and certain few nucleoli. The large ones vary in size from 9 to 11 μ in diameter.

Vacuolization proceeds intensely. Cell boundaries are obscure and staining affinity of the cytoplasm is relatively strong.

Apis mellifera adansonii — (worker)

Corpora alata are quite spherical. The large nuclei occur in high proportion. Their nucleoplasm is dark. They measure 12 to 14 μ in their longer axis. Small ones are also darkly stained and rich in chromatin. Large vacuoles are commonly observable around the nuclei. Cytoplasm is weakly stained and is finely granular. Cell boundaries are not distinct.

Apis mellifera adansonii — (queen)

Corpora alata are spherical. The large nuclei have much chromatin but generally less than those of workers. Cell boundaries are often indistinct. Vacuolization is extreme.

Apis mellifera ligustica — (worker)

Corpora alata are almost spherical. The large nuclei occur in high proportion and have their nucleoplasm clear but often very rich in chromatin. Cell boundaries are always distinct and active vacuolization occurs around the nuclei. Cytoplasm stains strongly with eosin.

Apis mellifera ligustica — (queen)

Corpora alata are almost spherical. Nuclei contain less chromatin and vacuolization is weaker than in workers. Cell boundaries are rather indistinct.

Discussion and conclusions

Among the studied material, species such as: *T. (Cephalotrigona) femorata; T. cilipes cilipes; T. hyalinata bruneri; T. (Tetragona) dorsalis; T. (Frieseomelitta) varia geneoscantha; T. (Ptilotrigona) lurida; Scaura (Scaura) tenuis; M. compressipes manaosensis; M. marginata amazonica; M. pseudocentris pseudocentris; M. seminigra merrillae,* which were collected at Manaus and were prefixed in Kahle's solution, showed *corpora alata* flattened to varying degrees. But with the fresh materials flattened or oval forms also occur sometimes, for example in *T. spinipes; T. (Frieseomelitta) flavicornis; T. (Tetragonisca) jaty; T. (Plebeia) droryana; T. (Partamona) pearsoni; T. (Scaptotrigona) postica* and *M. marginata marginata.* Therefore the general flattening in the Amazonian species may be an artefact of fixation, but may be to the same extent a real phenomena.

In previous papers, it has already been shown that in some stingless bee species worker ovaries develop even in queen right colonies contrary to the case of *Apis* (Sakagami & *al.*, 1963; Akahira, in press); moreover, the curious fact has been noted that eggs laid by the workers serve as food for the mature queen (Sakagami, S.F. & Zucchi, R., 1963). On the other hand, in the other stingless bee species well developed worker ovaries are never found. In *Apis* it has been observed (unpublished) that worker ovarioles just after emergence are slightly more swollen that in foragers. With respect to their development worker ovaries could be classified in three categories (see also table 2):

1) Worker ovaries do not develop at all: *T. (Trigona) crassipes; T. (Frieseomelitta) flavicornis; T. (F.) freiremaiai; T. (F.) varia geneoscantha; T. (Duckeola) ghilianii; T. (Ptilotrigona) lurida; T. (Partamona) nigrior; T. (P.) pearsoni;* and *T. (P.) testacea testacea;* additionally, *Hypotrigona müllerii,* examined by Sakagami.

2) Worker ovaries develop well: *T. (Cephalotrigona) femorata; T. (Trigona) spinipes; T. (Tetragona) dorsalis; T. (Tetragonisca) jaty; T. (Plebeia) droryana; T. (Friesella) schrottkyi; T. (Scaptotrigona) bipunctata; T. (S.) postica; T. (S.) xanthotricha;* and *Melipona* group (in which are included of *M. nigra shencki,* and *M. rufiventris.*

3) Worker ovaries develop partially; condition is yet uncertain *T. cilipes cilipes; T. hyalinata bruneri; Scaura (Scaura) tenuis* and *Meliponula bocandei.*

In table 2 these categories are denoted by "x", "o" and "?" respectively.

Although it is quite difficult to determine the degree of *corpora alata* activity, for convenience we select the following characters as being relevant and divide each into four classes:

a) % of large nuclei in the total number; when % increase activity of nuclei seems to be high. The 4 classes are: 1= less than 10%, 2= between 10 and 20%; 3= between 20 and 30%; 4= more than 30%.

b) cell volume (C. V.). When large activity of *corpora alata* seems to be high. Classes: 1= less than 3 μ^3, 2= between 3 and 5 μ^3; 3= between 5 and 7 μ^3; 4= more than 7 μ^3.

c) Volume index (V. I.). When large *corpora alata* are probably more active. Classes: 1= less than 50; 2= between 50 and 75; 3= between 75 and 100; 4= more than 100.

d) Quantity of chromatin in large nucleus. In general when chromatin is scarce, nuclear activity seems to be high. Subjectively we have distinguished 4 classes: 1= very large amount of chromatin; 2= large amount of chromatin; 3= quantity is more or less; 4= poor chromatin.

e) Vacuolization in cytoplasm. When it is pronounced, activity of the cytoplasm seems to be high. But, according to Palm (1948), the occurrence of vacuoles might be an artfact; and with the same microtechnique and in the same species its occurrence frequently varies. Especially when we compare with the case of another gland, for example the pharyngeal gland, it seems the more possible that the vacuoles may have contained some secretion which has dissolved out in the solvent, alcohol or xylol. This character is into 4 classes subjectively: 1= no vacuoles; 2= little amount of vacuoles; 3= active vacuoles; 4= large amount of vacuoles.

It must be admitted that the characters and especially the classes in the table 2 are largely arbitrary; we do not even know which characters are the more important; nevertheless we believe that the major tendencies in activity of the *corpora alata* are correctly indicated in this table.

There are five subgenera each having 3 or more species. In *Apis* two subspecies are included.

Trigona (cilipes cilipes; crassipes; hyalinata bruneri; spinipes), Frieseomelitta (flavicornis; freiremaiai; varia geneoscantha) Partamona (cupira; nigrior; pearsoni; testacea testacea). Scaptotrigona (bipunctata; postica; xanthotricha), Melipona (compressipes manaosensis; marginata marginata; marginata amazonica; pseudocentris pseudocentris; quadrifasciata anthidioides; quinquefasciata; seminigra merrillae), Apis (mellifera adansonii; mellifera ligustica).

1. In general the members of each subgenus tend to be similar; for example, in the *Melipona*-group similarity seems closely trough each of the characters studied, although *compressipes manaosensis* and *seminigra merrillae* are slightly excentric.

2. Among the groups, *Apis* and *Frieseomelitta (T. F. varia geneoscantha* is excepcional) seem to have extremely high activities of *corpora alata;* follows the *Partamona*-group which shows fairly high activities, and finally the group of *Scaptotricha* follows. On the other hand, the *Melipona* and *Trigona*-groups appear to have low activities of *corpora alata.*

3. When we compare the characters of *corpora alata* with the development of worker ovaries, the following hypothesis seems to be suported: There is an inverse correlation between activity of *corpora alata* and development of worker ovaries. If a species has a high activity of *corpora alata,* worker ovaries do not develop. Conversely, in the case of low activity, worker ovaries are found well developed. Cases conforming with the above hypothesis are as follows: *Frieseomelitta*-group, *Partamona*-group, *Melipona*-group, *Apis*-group, *T. spinipes, T. (Friesella) schrottkyi,* and *T. (Nannotrigona) testaceicornis:* amounting to 19 species. Contrary are the three species, *T. crassipes, T. (Tetragonisca) jaty,* and *T. (Plebeia) droryana.* There remains the group showing moderate activity of *corpora alata,* the *Scaptotrigona*-group, *T. (Cephalotrigona) femorata, T. (Tetragona) dorsalis* and *T. Duckeola) ghilianii,* amounting to 6 species; which nevertheless has typical well developed worker ovaries, with the exception of *T. (Duckeola) ghilianii.* Thus perhaps this level of moderate activity may mark the threshold for development of worker ovaries.

It is interesting that in the *Trigona*-group the relation between activities of *corpora alata* and worker ovaries is indistinct. Thus *T. crassipes* and *T. spinipes* are opposite in ovary development although both have low levels of *corpora alata* activity.

Among the species whose ovary development is as yet unknown, the four species *T. cilipes cilipes, T. hyalinata bruneri, Scaura (Scaura) tenuis* and *Meliponula bocandei* have low activity of *corpora alata,* lower even than of the *Scaptotrigona*-group. On the basis of our hypothesis therefore we might risk the prediction that these will prove to have developed ovaries. This will be matter for future researches.

In a previous paper it has been established that the development of worker ovaries followed a normal curve, that is, maximal development of worker ovaries occurs in the stage of nurse bee (Sakagami, 1963). Furthermore it has been observed that in the case of *T.* (*Scaptotrigona*) *postica,* one of the species showing typical ovary development, ovaries begin to grow 5 days after emergence, and maximal development comes 10 to 14 days after emergence. Subsequently ovaries undergo gradual degeneration which corresponds closely to the differentiation of labour, i. e., nurse workers becoming foragers (Sakagami & Akahira, unpublished data). We used only foragers in the present investigations on *corpora alata* and how the growth cycle of *corpora alata* corresponds to that of the ovaries remains for subsequent study. But however this may turn out, a correlation between *corpora alata* activity and worker ovary development seems certain.

It is well known experimentally in other insects that the *corpora alata* produce a "juvenile hormone" tending to inhibit the realization of imaginal characters during development, while in the last immature stages the *corpora alata* become inactive and a new hormonal balance influences metamorphosis (Wigglesworth, 1956). In this field nothing has yet been established experimentally for the stingless bees, but in those species belonging to the type having undeveloped worker ovaries it would seem possible that active *corpora alata* may continue to secrete something like "juvenile hormone" and that the worker ovaries may be inhibited by it. On the other hand, the so-called "ectohormone" or queen substance of *Apis* has special effects on the development of worker ovaries of stingless bees (Akahira, Y., S. F. Sakagami & W. E. Kerr, in press). Thus, though hormonal controls on ovary development have not as yet received much attention in stingless bees, they will certainly prove one of the important factors in the complex interaction of social life in this group of Hymenoptera.

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TABLE 1 — RESULTS OF BIOMETRICAL OBSERVATION (A)

	T. (Cephalotrigona) femorata							*Trigona cilipes cilipes*						
	N	N'	W	H	D	V	P	N	N'	W	H	D	V	P
1	85	16	78	17	49	393	1	23	8	31	17	21	59	1
2	69	16	82	18	49	413	1	25	1	50	12	21	75	1
3	68	16	90	20	49	430	2	17	3	34	15	28	85	2
4	59	16	85	20	35	356	2	33	6	42	15	28	91	2
5	46	10	71	18	35	280	3	30	10	47	15	28	132	3
6	76	21	78	15	49	348	4	41	10	34	15	35	107	3
7	65	18	58	17	42	230	5	55	23	54	18	42	242	4
8	67	6	71	21	49	378	6	50	18	54	17	49	210	4
9	71	8	79	18	42	344	7	34	6	29	14	28	78	5
10	72	8	51	28	35	325	8	24	8	28	14	28	56	5
X	67.8	13.5	74.3	19.2	43.4	349.7		33.2	9.3	40.3	15.2	30.8	111.5	
%		19.9							28.0					
C.V.						5.15							3.41	
V.I.						25.29							28.77	

	Trigona crassipes							*T. hyalinata bruneri*						
	N	N'	W	H	D	V	P	N	N'	W	H	D	V	P
1	56	7	54	21	35	180	1	47	10	58	15	49	200	1
2	47	8	64	18	21	119	1	54	13	70	15	35	204	1
3	33	8	53	15	21	111	2	42	18	75	14	28	148	2
4	47	8	45	21	21	117	2	34	8	62	12	21	96	2
5	70	5	51	14	42	175	3							
6	43	9	56	29	21	166	4							
7	54	22	43	14	35	113	5							
8	21	9	43	12	28	80	6							
9	55	11	56	18	28	170	7							
10	46	6	37	14	28	84	8							
X	47.2	9.3	50.2	17.6	30.4	131.5		44.2	12.2	66.2	14.5	33.2	162.0	
%		19.7							27.6					
C.V.						2.78							3.66	
V.I.						24.96							27.70	

	T. spinipes							*T. (Tetragona) dorsalis*						
	N	N'	W	H	D	V	P	N	N'	W	H	D	V	P
1	53	3	49	21	42	215	1	41	15	43	14	35	121	1
2	53	2	40	23	28	156	1	53	11	43	15	35	122	1
3	68	6	33	25	35	182	2	35	7	49	18	28	139	2
4	72	4	39	18	49	183	2	40	5	49	15	35	141	2
5	46	1	45	12	28	103	3	34	15	26	14	49	94	3
6	70	13	39	22	49	238	3	43	16	29	18	49	120	3
7	91	2	42	30	28	202	4	37	9	34	15	28	79	4
8	73	3	39	25	42	237	4	39	17	35	15	28	90	4
9	69	6	34	21	42	184	5	33	8	37	17	21	76	5
10	56	7	35	28	35	189	6	46	12	49	20	28	133	6
X	65.1	4.7	39.5	22.5	37.8	188.4		40.1	11.5	39.4	16.1	33.6	111.5	
%		7.2							28.1					
C.V.						2.89							2.78	
V.I.						39.70							58.49	

TABLE 1 — RESULTS OF BIOMETRICAL OBSERVATION (B)

	T. (Frieseomelitta) flavicornis							*T. (F) freiremaiai*						
	N	N'	W	H	D	V	P	N	N'	W	H	D	V	P
1	33	14	42	32	28	229	1	69	12	45	35	49	403	1
2	33	11	37	26	35	175	1	67	14	47	47	42	527	1
3	22	12	34	23	28	149	2	27	22	43	42	35	365	2
4	28	8	37	27	21	129	2	38	20	56	42	42	474	2
5	31	9	43	28	35	231	3	69	3	42	37	35	350	3
6	34	11	35	25	28	143	3	71	18	49	42	35	448	3
7	38	7	43	21	35	203	4	64	11	40	35	42	322	4
8	28	8	28	26	35	155	4	48	11	45	39	42	396	4
9	23	4	37	18	21	88	5	65	9	42	35	42	341	5
10	39	22	43	32	42	344	6	72	4	47	32	28	287	5
X	30.9	10.6	37.9	25.8	30.8	184.6		59.0	12.4	45.6	38.6	39.2	391.3	
%		34.6							21.0					
C.V.						5.97							6.63	
V.I.						101.70							205.29	

	T. (F) varia geneoscantha							*T. (Duckeola) ghilianii*						
	N	N'	W	H	D	V	P	N	N'	W	H	D	V	P
1	40	12	54	29	28	242	1	68	8	47	26	92	269	1
2	36	12	49	32	28	246	1	104	18	59	49	42	730	1
3	33	11	40	23	35	162	2	111	23	56	51	56	894	2
4	35	10	53	20	28	159	2	102	15	59	54	42	805	2
5	44	0	70	17	28	157	3	75	17	50	40	28	327	3
6	21	5	45	23	14	98	4	92	16	51	42	49	593	4
7	35	8	45	17	21	114	5	111	14	60	40	49	759	5
8								95	11	59	39	42	598	6
9								99	9	49	39	28	320	7
10								113	11	59	50	56	926	8
X	34.8	8.3	50.8	27.0	26.0	168.2		97.0	14.2	54.9	43.0	43.4	621.7	
%		23.8							14.6					
C.V.						4.83							6.40	
V.I.						61.29							56.82	

	T. (Tetragonisca) jaty							*T. (Ptilotrigona) lurida*						
	N	N'	W	H	D	V	P	N	N'	W	H	D	V	P
1	92	10	37	28	21	126	1	37	0	53	20	28	162	1
2	36	11	35	20	21	96	1	28	7	53	14	21	108	1
3	39	7	40	29	28	199	2	53	5	53	10	35	115	2
4	40	5	34	28	21	128	2	50	5	58	10	35	120	2
5	47	3	35	23	28	138	3	38	9	52	13	35	142	3
6	38	6	32	20	28	104	3	40	0	56	15	35	139	3
7	48	10	31	26	28	122	4	33	4	39	14	28	94	4
8	30	2	39	23	21	98	4							
9	45	3	31	25	21	110	5							
10	44	11	40	18	28	121	6							
X	40.9	6.8	35.4	24.0	24.5	124.2		39.8	4.3	52.0	13.7	31.0	125.7	
%		16.6							10.8					
C.V.						3.03							3.15	
V.I.						104.28							35.80	

TABLE 1 — RESULTS OF BIOMETRICAL OBSERVATION (C)

	Scaura (Scaura) tenuis							*Trigona (Plebeia) droryana*						
	N	N'	W	H	D	V	P	N	N'	W	H	D	V	P
1	32	13	34	14	35	93	1	24	4	29	18	28	93	1
2	30	11	39	12	28	67	1	17	3	29	18	21	63	1
3								24	6	29	21	21	83	2
4								20	8	29	21	28	94	2
5								23	6	32	23	21	105	3
6								22	6	32	17	21	80	3
7								29	5	28	26	21	86	4
8								27	5	28	26	21	98	4
9								19	2	26	21	21	84	5
10								24	3	32	20	28	97	5
X	31.1	12.0	36.5	13.0	32.5	80.0		32.9	4.8	29.4	21.1	23.1	88.3	
%		38.7							20.9					
C.V.						2.58							3.85	
V.I.						56.98							78.80	

	T. (Friesella) schrottkyi							*Trigona (Partamona) cupira*						
	N	N'	W	H	D	V	P	N	N'	W	H	D	V	P
1	23	3	20	18	28	46	1	9	4	34	21	28	121	1
2	25	7	21	20	21	62	1	28	5	31	26	35	147	1
3	34	2	32	23	14	80	2	48	14	60	43	35	536	2
4	33	2	31	23	14	75	2	38	14	56	49	28	470	2
5	33	3	39	29	7	62	3	34	10	35	32	21	134	3
6	28	4	35	28	14	97	3	32	9	28	21	28	102	3
7	15	3	28	17	19	39	4	51	18	50	39	42	451	4
8	20	6	26	15	21	51	4	43	18	59	42	42	585	5
9	14	4	25	14	14	32	5	45	17	59	41	42	434	6
10	19	6	25	20	14	49	6	46	13	32	20	42	144	7
X	24.4	4.0	28.2	20.7	16.1	59.3		7.4	12.2	44.4	33.4	34.3	312.4	
%		16.3							32.6					
C.V.						2.43							8.35	
V.I.						52.90							51.82	

	Trigona (Partamona) nigrior							*Part. (Partamona) pearsonii*						
	N	N'	W	H	D	V	P	N	N'	W	H	D	V	P
1	36	14	54	47	35	467	1	28	18	49	21	28	175	1
2	38	11	45	40	28	308	1	51	21	50	31	28	235	1
3	56	17	53	45	42	472	2	50	19	47	34	35	318	2
4	43	6	49	35	35	377	2	22	10	40	23	21	127	2
5	42	13	45	35	28	306	3	45	18	45	23	43	235	3
6	36	12	49	45	28	373	3	54	16	43	23	42	209	3
7	39	16	39	34	35	298	4	57	21	40	23	56	291	4
8	42	14	50	32	35	319	5	33	10	31	20	35	132	4
9	44	21	42	32	42	326	6	60	19	53	39	35	404	5
10	41	11	39	18	35	141	7	29	14	43	35	14	152	6
X	41.7	13.5	41.1	36.3	34.3	338.7		42.9	16.6	44.1	27.2	33.6	227.8	
%		32.3							38.6					
C.V.						8.12							5.31	
V.I.						62.13							29.34	

TABLE 1 — RESULTS OF BIOMETRICAL OBSERVATION (D)

	Trigona (P) testacea testacea							*Trigona (N) testaceicornis*						
	N	N'	W	H	D	V	P	N	N'	W	H	D	V	P
1	54	20	64	17	35	196	1	35	7	32	23	28	113	1
2	49	19	56	20	28	180	1	45	6	35	25	35	177	1
3	58	21	59	14	42	200	2	52	9	32	31	21	150	2
4	52	19	67	17	35	192	2	54	6	32	28	21	118	2
5	49	17	79	15	28	203	3	42	14	35	25	35	172	3
6	54	19	79	12	35	185	3	40	11	35	26	28	161	3
7	46	22	68	12	42	190	4	47	10	31	23	28	116	4
8	63	17	45	17	56	246	4	43	0	35	20	21	91	4
9	39	21	49	17	35	158	5	37	8	40	29	21	149	5
10	42	19	54	15	35	153	5	38	5	34	25	14	86	6
X	50.6	19.4	62.0	15.6	37.1	190.3		43.3	7.6	34.1	25.5	25.2	133.3	
%		38.3							17.5					
C.V.						3.76							3.07	
V.I.						52.10							36.50	

	T. (Scaptotrigona) bipunctata							*T. (S) postica*						
	N	N'	W	H	D	V	P	N	N'	W	H	D	V	P
1	52	15	40	29	42	276	1	55	10	38	30	40	257	1
2	49	20	34	31	42	230	1	40	10	38	31	24	176	1
3	44	2	48	28	42	284	2	53	13	39	34	40	355	2
4	38	2	40	20	35	170	2	43	10	37	37	32	269	2
5	39	4	30	27	28	132	3	63	14	50	28	40	312	3
6	24	2	31	15	28	72	3	55	14	50	28	48	339	3
7	57	10	36	25	35	172	4	40	11	39	24	28	143	4
8	24	1	34	27	28	114	4	46	10	31	26	28	147	5
9	59	19	31	28	35	186	5	52	8	40	28	42	289	6
10	65	21	40	33	42	314	6	44	20	39	32	40	280	7
X	41.5	9.6	36.4	26.3	35.7	195.0		49.1	12.0	40.1	29.8	36.2	256.7	
%		21.2							24.4					
C.V.						4.32							5.22	
V.I.						35.77							47.09	

	T. (S) xanthotricha							*Meliponula bocandei*						
	N	N'	W	H	D	V	P	N	N'	W	H	D	V	P
1	66	10	42	31	42	332	1	57	3	49	28	49	396	1
2	28	1	30	27	35	167	1	94	2	52	35	56	660	1
3	59	16	40	31	42	299	2	62	2	49	33	35	346	2
4	54	11	39	30	35	240	2	61	3	52	33	49	420	2
5	55	8	46	33	35	302	3	98	4	52	31	56	511	3
6	72	18	44	34	49	398	3	98	2	49	36	49	511	3
7	58	9	48	30	49	337	4	65	14	40	36	35	283	4
8	51	8	35	32	35	251	5	74	5	52	28	56	356	4
9	54	7	40	31	49	315	6	84	20	49	38	49	509	5
10	64	14	38	28	42	224	7	65	11	45	27	42	261	5
X	56.1	10.2	40.2	30.7	41.3	286.5		75.8	6.6	48.9	32.5	47.6	425.3	
%		18.1							8.7					
C.V.						5.10							5.61	
V.I.						52.55							23.20	

TABLE 1 — RESULTS OF BIOMETRICAL OBSERVATION (E')

	Melipona compressipes manaosensis							*M. marginata amazonica*						
	N	N'	W	H	D	V	P	N	N'	W	H	D	V	P
1	122	18	70	47	42	702	1	103	8	54	37	35	381	1
2	121	18	67	49	42	703	1	70	6	47	37	21	260	1
3	128	27	90	29	56	795	2	85	14	62	31	35	349	2
4	134	31	85	32	63	940	2	72	13	53	39	21	288	2
5	126	25	71	49	63	1199	3	90	8	47	40	35	357	3
6	132	17	59	50	63	1016	3	89	4	56	26	35	284	3
7	99	18	85	35	42	710	4	80	6	60	34	28	326	4
8	112	19	85	34	42	715	4	72	8	53	40	21	309	4
9	102	19	70	45	35	654	5	100	8	56	31	42	440	5
10	106	19	64	40	49	656	5	96	10	53	39	35	421	6
X	118.2	21.1	74.6	41.0	49.7	809.0		85.7	8.5	54.1	35.4	30.8	341.5	
%		17.8							9.9					
C.V.						6.84							3.98	
V.I.						38.47							25.98	

	M. marginata marginata							*M. pseudocentris pseudocentris*						
	N	N'	W	H	D	V	P	N	N'	W	H	D	V	P
1	98	10	40	35	56	403	1	51	10	35	14	42	114	1
2	86	4	43	31	35	311	1	48	9	34	14	92	111	1
3	65	7	36	27	35	205	2	43	9	53	15	28	117	2
4	79	6	33	26	49	224	2	31	5	43	10	21	60	2
5	63	9	38	26	42	248	3	45	11	51	12	35	131	3
6	69	3	40	26	28	202	3	47	7	65	10	21	84	4
7	108	7	44	26	49	319	4	33	6	56	13	21	79	5
8	110	12	46	24	49	276	4	36	8	55	12	28	86	6
9	74	23	46	34	42	392	5	53	7	32	12	35	88	7
10	111	7	40	34	49	369	6	22	7	31	12	35	77	8
X	86.3	8.8	40.6	28.9	43.4	294.9		40.9	7.9	45.5	12.4	30.8	94.7	
%		10.1							19.3					
C.V.						3.41							2.31	
V.I.						29.26							3.24	

	M. quadrifasciata anthidioides							*M. quinquefasciata*						
	N	N'	W	H	D	V	P	N	N'	W	H	D	V	P
1	71	15	48	24	42	289	1	134	16	75	32	49	662	1
2	114	24	82	90	42	719	1	138	7	73	31	49	575	1
3	115	17	62	36	35	498	2	117	12	65	34	42	568	2
4	124	18	64	38	35	482	2	93	5	62	75	42	855	2
5	131	12	50	45	56	740	3	122	9	97	23	49	560	3
6	101	22	60	23	35	292	4	97	2	85	31	28	397	3
7	101	11	39	42	35	543	5	121	21	95	29	42	509	4
8	92	21	49	34	49	450	6	118	20	73	28	42	491	4
9	141	23	58	35	49	591	7	98	8	58	40	49	645	5
10	121	9	45	34	49	305	8	95	8	73	31	35	421	6
X	113.0	17.2	57.7	35.1	42.9	490.9		113.3	10.8	73.6	30.4	42.7	518.3	
%		15.2							9.5					
C.V.						4.34							4.57	
V.I.						16.16							17.06	

TABLE 1 — RESULTS OF BIOMETRICAL OBSERVATION (F)

	M. seminigra merrillae							*Apis mellifera adansonii* (worker)						
	N	N'	W	H	D	V	P	N	N'	W	H	D	V	P
1	209	32	81	51	63	1333	1	77	26	84	68	70	2115	1
2	181	34	79	47	56	1171	1	104	25	90	82	56	2408	1
3	187	25	85	31	49	805	2	94	34	84	79	84	2846	2
4	176	28	84	42	56	886	2	102	36	85	68	84	2574	2
5	146	28	82	31	70	928	3	60	17	92	71	49	1886	3
6	116	24	85	26	63	736	3	89	26	89	64	70	1541	3
7	95	34	84	28	70	929	4	98	28	89	73	63	2175	4
8	131	26	90	35	63	919	4	85	25	92	82	70	2893	4
9	176	27	65	49	70	1002	5	108	29	93	71	70	2544	5
10	205	20	98	53	56	1404	5	109	27	82	71	84	2842	5
X	162.2	27.8	83.3	39.3	61.6	1011.3		92.6	27.3	88.0	72.9	70.0	2382.4	
%		17.1							29.4					
C.V.						6.23							25.72	
V.I.						34.61							75.50	

	A.m. adansonii (queen)							*A.m. lingustica* (worker)						
	N	N'	W	H	D	V	P	N	N'	W	H	D	V	P
1	114	29	129	106	77	5189	1	100	34	120	108	84	5764	1
2	124	39	118	93	70	3997	1	101	33	120	103	84	5632	1
3	166	74	136	129	112	10872	2	85	31	90	70	70	2628	2
4	165	63	138	134	112	11200	2	104	30	97	81	63	2837	2
5								116	35	125	95	84	5251	3
6								131	41	129	103	91	6214	3
7								113	25	93	81	70	3158	4
8								124	32	118	95	91	6020	4
9								107	33	101	82	84	4020	5
10								86	28	82	76	56	2189	5
X	142.2	51.2	130.2	115.5	92.7	7814.5		106.7	32.2	107.5	89.4	77.7	4371.3	
%		36.0							30.1					
C.V.						45.05							40.96	
V.I.						286.50							138.53	

	A.m. lingustica (queen)						
	N	N'	W	H	D	V	P
1	47	25	106	87	63	3128	1
2	51	12	75	60	49	1211	1
3	180	35	118	75	70	3141	2
4	148	38	123	78	56	3192	2
X	119.0	27.5	150.5	75.0	58.7	2668.0	
%		23 1					
C.V.						22.42	
V.I.						97.83	

TABLE 2 — RELEVANT CHARACTERS THAT SUMARIZED THE DEGREE OF CORPORA ALLATA ACTIVITY AMONG THE TRIBLES TRIGONINI, MELIPONINI AND APINI

Characteristic.	TRIGONA																							
	CF	TCC	TCr	THB	TS	TDo	TFl	TF	TVG	TG	TJ	TL	ST	TD	TSc	TC	TN	TPe	TTT	TT	TB	TP	TX	MB
%	2	3	2	3	1	3	4	3	3	2	2	2	4	3	2	4	4	4	4	2	3	3	2	1
C.V.	3	2	1	2	1	1	3	3	2	3	2	2	1	2	1	4	4	3	2	2	2	3	3	2
V.I.	1	1	1	1	1	2	4	4	2	2	4	1	2	3	2	2	2	1	2	1	1	1	2	1
Chromatin	3	3	3	2	2	3	2	2	2	3	3	3	3	2	2	3	2	3	3	2	2	2	2	2
Vacuole	2	2	1	1	1	2	4	4	2	3	4	1	1	4	2	2	3	2	2	3	3	3	3	3
Sum	11	11	8	9	6	11	17	16	11	13	15	9	11	14	9	15	15	13	13	10	11	12	12	9
Ov. dev.	0	?	x	?	0	0	x	x	x	x	0	x	?	0	0	x	x	x	x	0	0	0	0	?

Characteristic.	MELIPONA							APIS			
	MCM	MMM	MMA	MPP	MQA	MQ	MSM	AMAw	AMAq	AMLw	AMLq
%	2	2	1	2	2	1	2	3	4	4	3
C.V.	3	2	2	1	2	2	3	4	4	4	4
V.I.	1	1	1	1	1	1	1	3	4	4	3
Chromatin	3	2	2	3	2	2	3	3	2	2	3
Vacuole	3	2	2	1	2	1	2	3	3	3	2
Sum	12	9	8	8	9	7	11	16	17	17	15
Ov. dev.	0	0	0	0	0	0	0	x	x	x	x

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