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Phylogenetic Significance of an Unusual African Stingless Bee, Meliponula bocandei (Spinola)

by

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The main purpose of this paper is, first, to show that a general knowledge of *Meliponula bocandei* is essential in obtaining a better and greater understanding of the phylogeny of the stingless bees, and second, to indicate the systematic position of this unusual African species.

Meliponula bocandei is found throughout most of Africa (Liberia, Nigeria, French Cameroons, Guinea, Congo, Uganda, Angola, Mozambique) where it is highly regarded by the people because of its honey, *M. bocandei* being the best producer among the African stingless bees. It is said that one nest can yield from 5 to 18 liters of good honey, and the bees are easy to handle. In general appearance *M. bocandei* looks like a rusty yellow-brown *Melipona* of almost a centimeter in length. Its tegument is minutely granulose, with the thorax covered with dense and short pilosity. A worker of *M. bocandei* can be easily differentiated from the other species by the very robust hind legs. The femur is stout and swollen; the tibia sub-spatulate, with the lower two-fifths concave, shiny, and slightly bent inwards, while the upper three-fifths is convex, swollen, dull, and finely granulose.

The species *M. bocandei* was described by SPINOLA (12) in 1853 and was regarded for many years as belonging to the genus *Trigona*. In 1934, however, COCKERELL (1) proposed *Meliponula* as a subgenus of *Melipona* to include *M. bocandei* and eight more species. Later, it was found that the additional eight species were not actually very close to *M. bocandei*. For this reason, *M. bocandei* became the only known species of the group *Meliponula* which was then raised to generic status. The fact that *M. bocandei* has been included both in the genus *Trigona* and in *Melipona* shows already that this species has an unusual set of characters.

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MAJOR EVOLUTIONARY TRENDS AMONG THE STINGLESS BEES

In order to analyze the position of *Meliponula bocandei* it is necessary to review the major evolutionary trends among the stingless bees. If we ignore for the moment the species *M. bocandei,* it is possible to distinguish two major and diverging lines among the stingless bees. For convenience these two evolutionary trends can be called the *Trigona* line and the *Melipona* line. That these two lines actually represent monophyletic lines is strongly indicated by the whole constellation of morphological and biological trends and characters by which these two groups can be separated. For the differences in morphology, reference should be made to Table 1, in which the main morphological differences are

TABLE 1

Morphological characters differentiating the Trigona *line from the* Melipona *line*

Characters	*Trigona* line	*Melipona* line
Size	usually small from 2 to 8 mm in length) and slender	Usually rather large (from 8 to 15 mm in length) and robust
Pubescence	usually short and sparse	upper half of head and thorax densely hairy, hairs long
Basal area of propodeum	usually glabrous, but sometimes tessellate and pubescent	tessellate and entirely pubescent
Length of fore wing	usually long and extending well beyond apex of abdomen	relatively short and not, or slightly surpassing tip of abdomen
Pterostigma	realtively broad, and distinctly rounded or convex below	poorly developed, narrow to linear, not rounded below
Submarginal angle (basal angle of first R cell)	variable	distinctly acute
Hamuli	usually from 5 to 8	from 9 to 16
Shape of hind tibia	variable	normal, without any type of depression
Nerve system	abdominal ganglion 3 located in first metasomal segement	abdominal ganglion 3 located in thorax
Dorsal vessel	thoracic portion straight	thoracic portion making an arch between longitudinal muscles of thorax

tabulated. In Table 2 the major biological characters are indicated. When a trend rather than an invariable character is described, the word "usually" is added.

TABLE 2

Biological characters differentiating the Trigona *line from the* Melipona *line*

Characters	*Trigona* line	*Melipona* line
Determination of workers and queens	presumably trophically determined	supposedly genetically determined
Size of the virgin queens	larger than workers, with a notably wider thorax, reared from larger royal cells	smaller than workers, especially in width of thorax, and reared from ordinary comb cells
Ovaries of the newly emerged queens	well developed	underdeveloped
Rate of production of queens	relatively rarely produced	frequently produced
Location of royal cells	near periphery of combs	intermingled in the combs with cells of workers and males
Nature of the nest entrance and batumen plates	usually made out of cerumen	usually made out of mud

Typically, the *Melipona* line is represented by the genus *Melipona* and the *Trigona* line by the genus *Trigona*. Other recognized genera are merely specialized branches of the *Trigona* line. These two evolutionary trends or lines have been regarded by MOURE (8) as tribes, namely, the Meliponini and Trigonini. However, we should point out that the gap between them is much smaller than that normally found between tribes (e.g., in those recognized by MICHENER (6). The narrowness of this gap is suggested by the difficulty many investigators encountered for almost a century in separating *Melipona* and *Trigona*. Although it is true that the separation of *Melipona* and *Trigona* has been made easier in recent years by the discovery of new and apparently valid taxonomic characters, such as those concerned with the dorsal vessel (WILLE, 14) and the ventral nerve cord (WILLE, 16), it is also true that the separation becomes apparently more difficult and uncertain when the characteristics of *M. bocandei* are considered. For this reason, a careful study of *M. bocandei* is necessary in order to obtain a better understanding of the general phylogeny of the stingless bees.

TRIGONA-LIKE CHARACTERS OF MELIPONULA BOCANDEI

Morphologically there are three structures in *Meliponula bocandei* which are typically *Trigona*-like. These structures are: the forewing, the hind tibia, and the ventral nerve cord.

FOREWING (Fig. 1): Although the length of the forewing in *M. bocandei* is not as great as the most typical *Trigona,* it is relatively long and extends beyond the apex of the abdomen. However, the feature which gives the forewing an unmistakable *Trigona*-like character is the pterostigma, which, even though small, is distinctly rounded below. Also the submarginal angle is slightly greater than 90º. In all the species of *Melipona* that are known the submarginal angle is slightly less than 90º.

HIND TIBIA (Fig. 2): The hind tibia of *M. bocandei* is definitely not of the *Melipona* type, since it is not triangular in shape, and lacks the posterior apical angle. On the contrary, the shape of the hind tibia in *M. bocandei* is subspatulate, with the distal posterior corner obliquely truncate and armed with a rastellum (comb, in MOURE's terminology, 8) made up of rather weak bristles. Furthermore, the inner side of the tibia has a posterior and slightly depressed bare strip, suggesting that of *Plebeia* and *Scaura.*

VENTRAL NERVE CORD (Fig. 3): In *M. bocandei* abdominal ganglion 3 is located in the first metasomal segment, as in all the species of *Trigona* and unlike *Melipona.* Moreover, ganglia 6 and 7 in *M. bocandei* are located in the fifth abdominal segment (fourth metasomal segment); these ganglia are very close, almost fused (Fig. 3, B). It should be pointed out that one of the two males dissected has ganglia 6 and 7 completely fused (Fig. 3, C), while, on the other hand, the other male had the same ganglia well separated, with ganglion 7 located in the sixth abdominal segment (Fig. 3, A). These differences in the two males are not very surprising, since it has been shown elsewhere that specimens occasionally differ somewhat from the normal types. It is possible, however, that our first male represents the normal type for the males and that the second is an abnormal example. Actually, the second case (Fig. 3 A) is a very primitive condition found previously (WILLE, 16) only in *Trigona fulviventris* Guérin. In any case, these two male examples illustrate the evolutionary trend in *M. bocandei* toward the fusion of abdominal ganglia 6 and 7 as shown in figure 3.

Biologically it seems that *M. bocandei* is similar to *Trigona* rather than to *Melipona.* At least, we know from the work of PORTUGAL-ARAÚJO (9) that the virgin queens of *M. bocandei* are larger than the workers, and are reared from specialized royal cells.

MELIPONA-LIKE CHARACTERS OF MELIPONULA BOCANDEI

Besides the *Trigona* characters discussed above, *Meliponula bocandei* also possesses certain important features which are typical of *Melipona.* These are general appearance, body surface, and the dorsal vessel.

GENERAL APPEARANCE: *M. bocandei* is a very robust bee of about 8 mm in length, with a short and stout abdomen that gives it an unmistakable appearance of *Melipona.* It seems appropriate to discuss here the number of hamuli, since, as has been shown by SCHWARZ (10), the number tends to be correlated with the size of the bee. Thus, species of small size usually have fewer hamuli, while species of more robust build frequently have a larger number. In *M. bo-*

candei the average number is nine; this number seems a consequence of the *Melipona*- like build. The size also explains the specimens of the largest *Trigona,* like *T. capitata* Smith and most *T. thoracica* Smith, which also have nine hamuli per wing.

BODY SURFACE: The integument of *M. bocandei* is in general tessellate, with the head, thorax and legs minutely granulose, and the abdomen finely dull-reticulate. But the character that makes the body surface of *M. bocandei* look like a *Melipona* is the pubescence, which, although short, is very dense on the upper half of the head and the thorax. The combination of this type of integument and pubescence results in the propodeum of *M. bocandei* being tessellate and pubescent, which is unlike most *Trigona,* but like all the species of *Melipona.*

DORSAL VESSEL (Fig. 4): In *M. bocandei* the thoracic portion of the dorsal vessel is arched between the dorsal longitudinal muscles of the thorax. As has been shown before (WILLE, 14), this type of dorsal vessel is typical of the genus *Melipona* and wholly unlike the genus *Trigona,* in which the thoracic portion of the dorsal vessel is straight and runs dorsal to the gut. Another interesting feature is the enlargement, in *M. bocandei,* of the last two chambers (Fig. 5, C), a character found previously (WILLE, 14) only in the Euglossini.

PRIMITIVE CHARACTERS IN **MELIPONA BOCANDEI**

In order to learn whether certain characters in *Meliponula bocandei* are primitive or specialized, it would be important to know the state of the characters in the bees presumed to be ancestral to *M. bocandei.* Since the ancestors of *M. bocandei* are presumably extinct and not known, it was necessary to determine the generalized and specialized state of its characters by comparing them with those which have been investigated in other bee groups. In general, any character found to be widely distributed among the stingless bees, and among other groups of bees, was considered primitive.

Actually, there are only a few primitive characters found in *M. bocandei.* One of them is the sting, which is better devoloped than in most Meliponini. As is well known, among the main specialized characters of the stingless bees is the reduction of the sting. Although it is ineffective in all the Meliponini, there exist several stages in its reduction. In *M. bocandei* we find the second valvulae fused into a short stylet and the first valvulae forming short lancets (Fig. 6, A). This type of sting may be regarded as the least reduced among the stingless bees, and it is found only in *M. bocandei* and a few other African bees, like *Trigona beccarii* Gribodo, *T. lendliana* Friese, *T. nebulata* Smith, and *T. conradti* Friese. The next step toward a further reduction of the sting apparatus is found in those bees in which the first and second valvulae are still more poorly developed, but with the valvulae directed upwards, forming an angle (Fig. 6, B). This type is found in the majority of the stingless bees. Finally, the maximum reduction of the sting is found in certain species of the subgenera *Tetragona* and *Trigona (T. acapulconis* Strand, *T. mombuca* Smith, *T. fulvohirta*

Friese, *T. carbonaria* Smith, *T. trinidadensis* (Provancher), *T. ruficrus* (Latreille), *T. corvina* Cockerell, and *T. nigerrima* Cresson). In this type the first and second valvulae are very poorly developed and are placed transversely and horizontally, without forming an angle (Fig. 6, C). It may be of some general interest to indicate that the gonostylus is flat in *M. bocandei* and in most African species of Meliponini. The evolutionary trend toward reduction of the sting apparatus is illustrated in figure 6.

Another character[1] in *M. bocandei,* regarded as very primitive by KERR and MAULE (5), is the brood food, which in this African species is very dry and uniform throughout, instead of being a mixture of pollen and honey with a top layer of clearer material (glandular food), as in most stingless bees.

The fact that *M. bocandei* arranges its brood cells more or less in clusters has also been regarded as an indication of primitiveness. However, it should be pointed out that the brood cells of *M. bocandei* have a strong tendency to form irregular horizontal combs, mixed with oblique and vertical layers. Furthermore, as MICHENER (7) has properly indicated, the cluster type of brood cell organization is not necessarily a primitive character. If the cluster type were actually so, then the combs must have arisen independently in several groups, which seems unlikely. On the other hand, disorganization of combs to produce the cluster type can easily have occured independently in several groups, as an adaptation for the use of small and irregular cavities as nesting sites.

In comparing *M. bocandei* with the species of the genus *Melipona,* it should be indicated that a ventral nerve cord with abdominal ganglion 3 located in the first metasomal segment, is of course, less specialized than the one with the abdominal ganglion 3 well inside the thorax, as in *Melipona.* Likewise, there is good evidence to regard the biology of the species of the *Trigona* line and *Meliponula* as less specialized than that of *Melipona.* If the genetic determination of the queen in *Melipona* is accepted as originating by a series of mutations from a *Trigona* ancestor, passing through three types of genetic segregation of castes, namely from a monofactorial to a trifactorial type (for details see KERR, 2, 3 and 4), then such characters as the frequency of the production of queens, subequal size of queens to that of the workers, lack of specialized royal cells, and the intermingled condition of the royal cells with those of the workers and males, can be explained as secondary adaptations to the genetic determination of the queen.

To summarize, in view of the facts that (1) in *M. bocandei* the virgin queens are larger than the workers, being presumably trophically determined, and (2) the sting, ventral nerve cord, and the brood food are still generalized, *M. bocandei* should be regarded as a less specialized bee than any of the species of *Melipona.*

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[1] Yet another character considered as primitive by KERR and LELLO in a paper (1962, *Jour. New York Ent. Soc.,* 70 : 190-214) published after completion of the present work is the very large poison sac containing oily liquid. Since this sac is of only moderate size in *Bombus, Apis,* and most other bees, its large size in *M. bocandei* seems to be a specialization.

SPECIALIZED CHARACTERS IN **MELIPONULA BOCANDEI**

Although *Meliponula bocandei* is seemingly more primitive than *Melipona,* it can still be considered a rather specialized bee, much more so than any species of the *Trigona* line. This is indicated by the following specialized characters found in *M. bocandei.*

1) Integument finely granulose and dull.
2) Upper half of head and thorax densely hairy.
3) Vertex strongly arched, raised behind the ocelli.
4) Propodeum almost entirely declivous and very small, concealed by the projecting scutellum when seen from above.
5) Hind femur conspicuously swollen.
6) Hind tibia very robust, with distal two fifths concave, shining, and slightly bent inwards, while the upper three fifths are convex, dull, and finely granulose.
7) Hind basitarsus strongly and acutely projecting distally.
8) Mesosternal apophysis well developed, with horizontal plate very wide (three times width of flagellum) and not declivous (its anterior portion about the same level as the posterior portion); vertical plate also very wide and rectangular in shape. The exceedingly well developed mesosternal apophysis of *M. bocandei* is probably correlated with the robust legs. The mesal promotor and remotor muscles of the middle coxa arise on the vertical plate of the apophysis, and the coxal retractor of the propectus on the horizontal plate.
9) Thoracic portion of dorsal vessel making an arch between dorsal longitudinal muscles of thorax (Fig. 4).
10) Last two chambers of heart enlarged. It is interesting to note than the beginning of this enlargement is found in the other stingless bees, in all of which the widths of the slightly enlarged chambers are less than half their lengths (Fig. 5, B). In *M. bocandei* the enlargement is more noticeable, and the widths of the chambers are half their lengths (Fig. 5, C). The trend toward the enlargement of the last two chambers culminates in the Euglossini, where there are found different stages of development. Thus, in *Eulaema dimidiata* (Fabricius), the widths of the enlarged chambers are equal to their lengths (Fig. 5, D). In *Euplusia coerulescens* (Lepeletier) the widths of the two enlarged chambers are slightly more than their lengths (Fig. 5, E). Finally, in *Euglossa cupreiventris* Cheesman the widths of the enlarged chambers are twice or more than twice their lengths (Fig. 5, F).
11) Storage pots hexagonal in shape, although they are circular when isolated.

DISCUSSION

As has been shown, *Meliponula bocandei* has a rather peculiar combination of characters, which are in many cases intermediate between the *Trigona* and

Melipona lines. As far as the author is aware, *M. bocandei* is the only species of the stingless bees possessing a ventral nerve cord typical of *Trigona* combined with a dorsal vessel typical of *Melipona.* In conclusion, the present study strongly suggests that this African species represents a third major phyletic line among the stingless bees. For this reason, if the *Trigona* and *Melipona* lines are recognized as tribes, then logically the *Meliponula* line should be also regarded as a tribe, the Meliponulini. However, as has been indicated before, the gap between these three evolutinoray lines is not sufficiently wide to justify raising them to tribes. Considering only phyletic relationships, the three major phyletic lines, namely, *Trigona, Meliponula* and *Melipona,* should be the recognized genera of the stingless bees. However, it is customary to base classification on degree of difference rather than on phyletic relationships. Because of varying evolutionary rates, such a classification is not always the same as one based on phylogeny. For example, it is customary to regard most parasitic derivatives ot major phyletic lines as distinct genera, because they are strikingly different from their nonparasitic relatives: *Psithyrus* is considered generically different from *Bombus,* and *Coelioxys* from *Megachile.* For the same reason, the robber bees derived from *Trigona* are given generic status as *Lestrimelitta,* its most distinctive morphological feature being the lack of corbicula, pecten and rastellum. In addition, *Dactylurina,* another derivative of *Trigona (Tetragona),* can also be regarded as a genus, mainly because of its peculiar elongate abdomen and its biology. *Dactylurina* is the only known stingless bee which constructs its broodcombs vertically, with cells on both surfaces, somewhat like those made by Apini (SMITH, 11). There is some justification for recognition of certain specialized side branches such as *Lestrimelitta* and *Dactylurina* as genera. Unfortunately, however, this practice can be carried to an extreme by regarding all minor specialized side branches as genera, and thus breaking up a genus unnecessarily.

Judging by the number of primitive characters and the lack of specialized features, *Plebeia* (including Moure's *Meliplebeia, Apotrigona, Plebeiella, Plebeina,* and *Austroplebeia)* and *Nogueirapis* should be regarded as the most primitive among the stingless bees (WILLE, 17). The earliest known Meliponini are from the middle Miocene, and judging by the amazing similarity of at least one of the fossil forms to the recent *Trigona* (WILLE, 15), one is compelled to believe in an earlier origin of the stingless bees. It is probable that they originated during the Eocene, when the modernization of flowering plants and the development of extensive forests took place. The earliest stingless bees were, no doubt, members of the *Trigona* line, which very likely were represented during that age by small *Plebeia*-like bees, all of which should have been already undergoing reduction of the sting apparatus and the veins of the fore wing. The warm and humid climate and the wide distribution of tropical forests during the Oligocene undoubtedly favored the adaptive radiation of the stingless bees. For this reason, it is likely that during this time another major trend may have started. This trend probably began with the development of larger size and denser hair in certain bees, in which the thoracic portion of their dorsal vessels eventually became arched between the longitudinal muscles. The beginning of this trend could be called the *Meliponula-Melipona* line (Fig. 7). Meanwhile the species of the *Trigona* line developed along various paths of adaptive radiation, giving origin to several minor side-branches, some of which in turn gave rise to other secondary branches. While this was taking place, cephalization of the ventral nerve cord must have begun in the *Meliponula-Melipona* line, thus initiating the differentiation of *Melipona*. This major change was followed by other minor morphological modifications, like the shortening of the wings, etc. A second step toward the modern *Melipona* was apparently a process which changed completely their basic reproductive biology. This was accomplished by a series of mutations which changed the trophogenic type of caste determination of these bees to one which is blastogenic or genotypic. The lateness of this change would explain why *Melipona* did not expand to other continents like the species of the *Trigona* line. Most queens of *Melipona* are trifactorial in their type of caste determination according to KERR (2); however, *M. marginata* Lepeletier was found to be bifactorial, and for this reason has been regarded by him as the most primitive species of *Melipona*. Because of this type of change, *Meliponula* and *Melipona* diverged to such an extent that they formed two separate major evolutionary lines (Fig. 7). *M. bocandei* can be regarded as the only species surviving from the early *Meliponula-Melipona* line. One of the possible reasons for its survival might have been the structural specialization undergone by this bee. It is interesting to note that KERR and MAULE (5) in a recent paper have expressed their opinion that the fossil *Meliponorytes*, described by TOSI (13) from the Sicilian amber, is related to *Meliponula*. Although this may be true, I am hesitant in accepting this view, since *M. bocandei* is a rather specialized bee, and Tosi's description of *Meliponorytes* is not sufficient to allow accurate comparisons.

SUMMARY

The African stingless bee, *Meliponula bocandei* (Spinola), is studied in relation to the general phylogeny of the Meliponini. The major evolutionary trends among the stingless bees, namely the *Trigona* and *Melipona* lines, are discussed, and *Meliponula bocandei* is compared with them. The morphological analysis of this species suggests an intermediate position for *Meliponula* between *Trigona* and *Melipona;* its biology, however, is apparently similar to that of *Trigona*. Consideration of the possibly primitive and specialized characters among bees indicates that *Meliponula* is more specialized than *Trigona* but less so than *Melipona*. It is therefore deduced that *Meliponula bocandei* represents another major phyletic stock, the *Meliponula* line.

Although the three major lines are considered in this study as the typical genera of Meliponini, there is also some justification in regarding as genera certain specialized side branches of the *Trigona* line *(Lestrimelitta, Dactylurina)*. Finally, a general discussion is given as to the possible ways these three major trends were differentiated, tracing their evolutionary history as far back in time as possible.

RESUMEN

El presente trabajo consiste en un estudio sobre la abeja africana, *Meliponula bocandei* (Spinola), en su relación a la filogenia general de los Meliponidos. Se discuten las tendencias evolutivas principales entre los Melipónidos, a saber, las líneas filogenéticas *Trigona* y *Melipona,* y se compara *Meliponula bocandei* con ambos géneros.

El análisis morfológico de esta especie sugiere una posición intermedia entre *Trigona* y *Melipona;* su biología, sin embargo, es aparentemente similar a la de *Trigona.* Un análisis de los posibles caracteres primitivos y especializados indica que esta especie es muy especializada, mucho más que *Trigona* pero menos que *Melipona.* De esto se deduce que *Meliponula bocandei* representa en realidad otra tendencia principal evolutiva: la línea filogenética *Meliponula.* Aunque las tres líneas filogenéticas principales se consideren en este estudio como representadas por los géneros típicos de los Melipónidos, existe alguna justificación para considerar como géneros a ciertas ramas especializadas *(Lestrimelitta* y *Dactylurina)* de la línea *Trigona.* Finalmente, se ofrece una discusión sobre la posible manera de diferenciación de las tres líneas principales, trazando su historia evolutiva hasta donde es posible.

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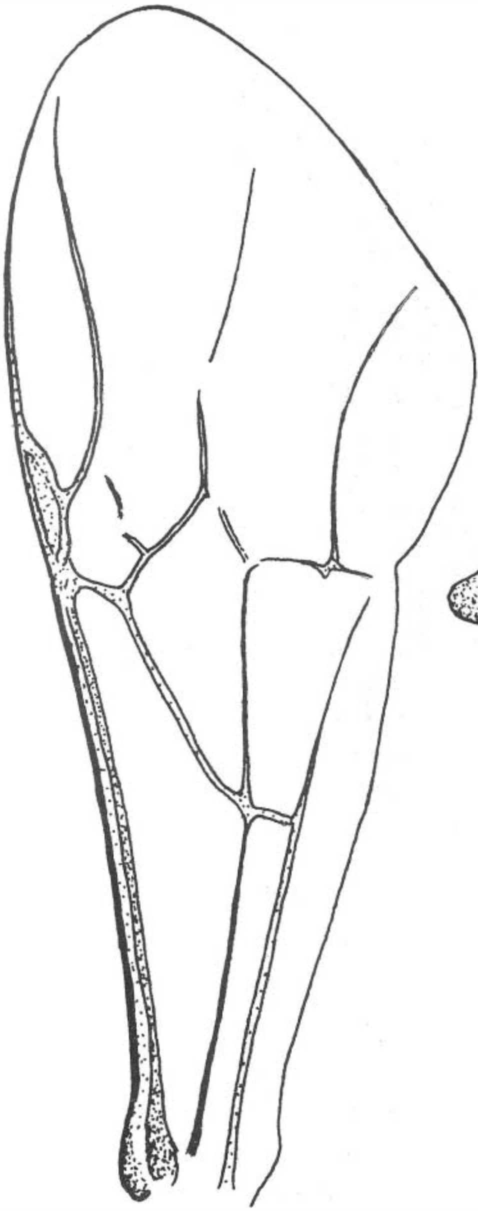
Figs. 1 and 2: *Meliponula bocandei*

Fig. 1: Right fore wing, hairs omitted.

Fig. 2: Outer surface of left hind tibia.



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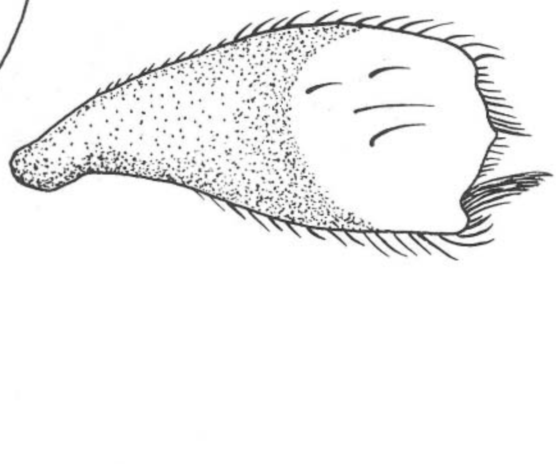

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Fig. 3: The ventral nerve cord of *Meliponula* showing the abdominal ganglion 3 located in the first metasomal segment (or second abdominal segment). Also showing the evolutionary trend toward the fusion of ganglia 6 and 7. I to III, thoracic ganglia; 1 G to 7 G, abdominal ganglia; 2 A to 8 A, abdominal segments. A. As in one male. B. As in most workers. C. As in another male.

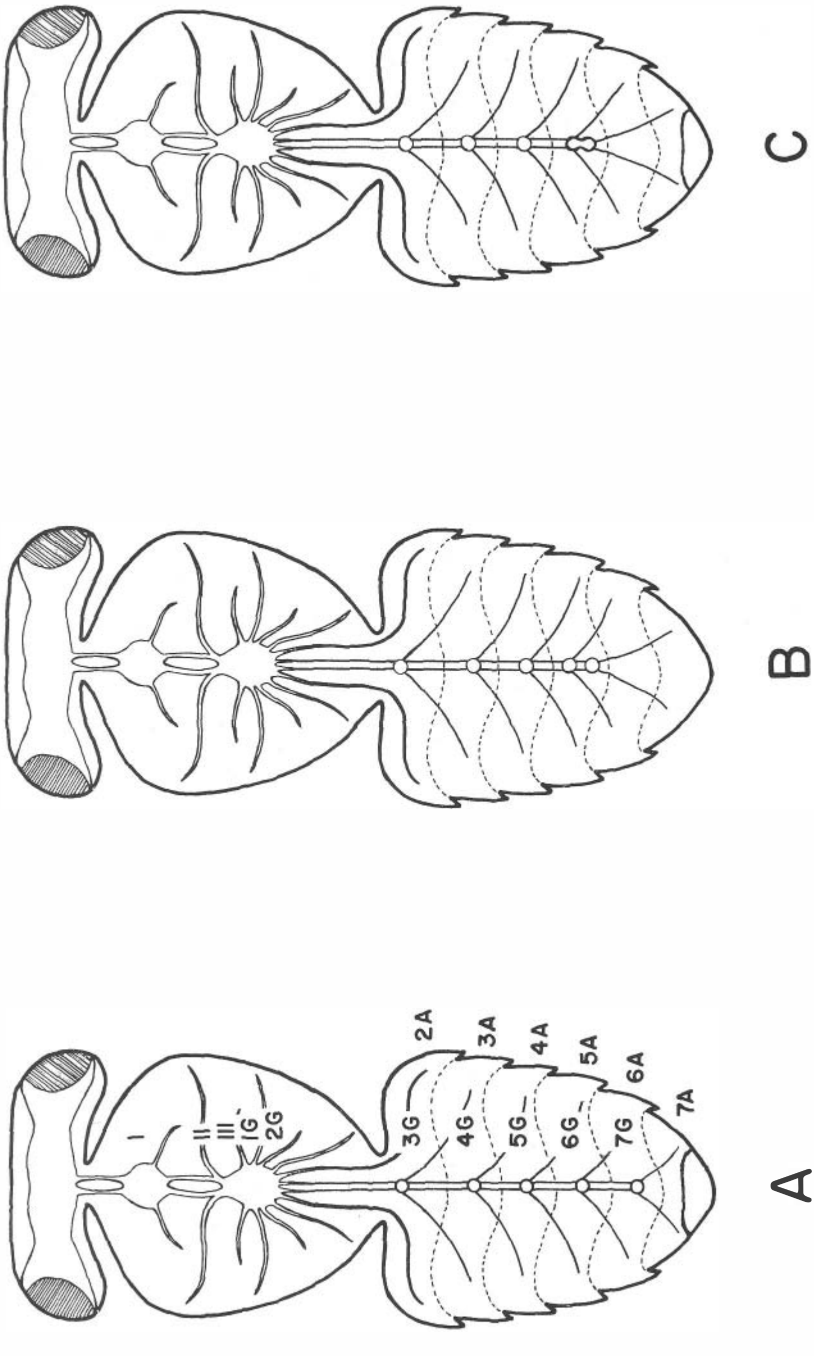

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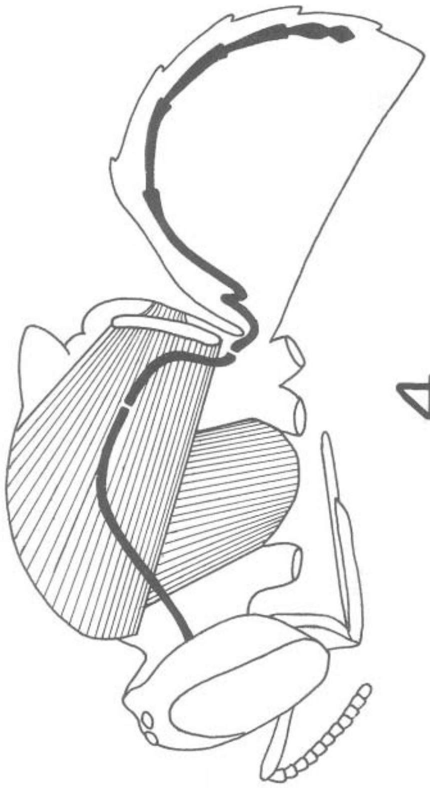
Fig. 4: The dorsal vessel of *Meliponula* showing the thoracic portion arched between the longitudinal muscles of the thorax.

Fig. 5: Evolutionary trend toward enlargement of the last two chambers of the heart. A. As in most bees. B. As in most stingless bees. C. As in *Meliponula bocandei*. D. As in *Eulaema dimidiata*. E. As in *Euplusia coerulescens*. F. As in *Euglossa cupreiventris*.



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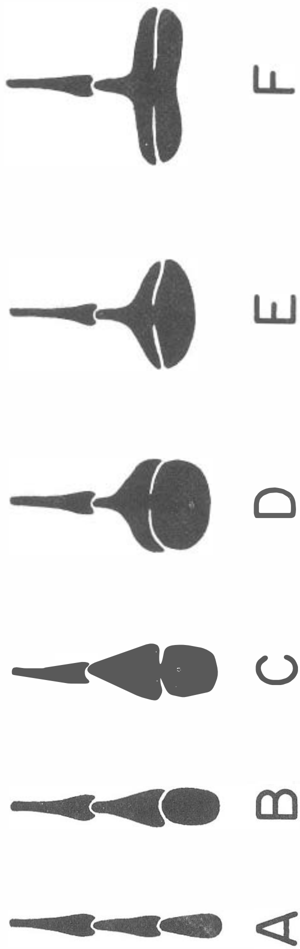

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Fig. 6: Evolutionary trend toward reduction of sting apparatus in the Meliponini.

A. As in *Meliponula bocandei* and a few other African bees (see text).

B. As in most stingless bees.

C. As in certain species of the subgenera *Tetragona* and *Trigona* (see text).

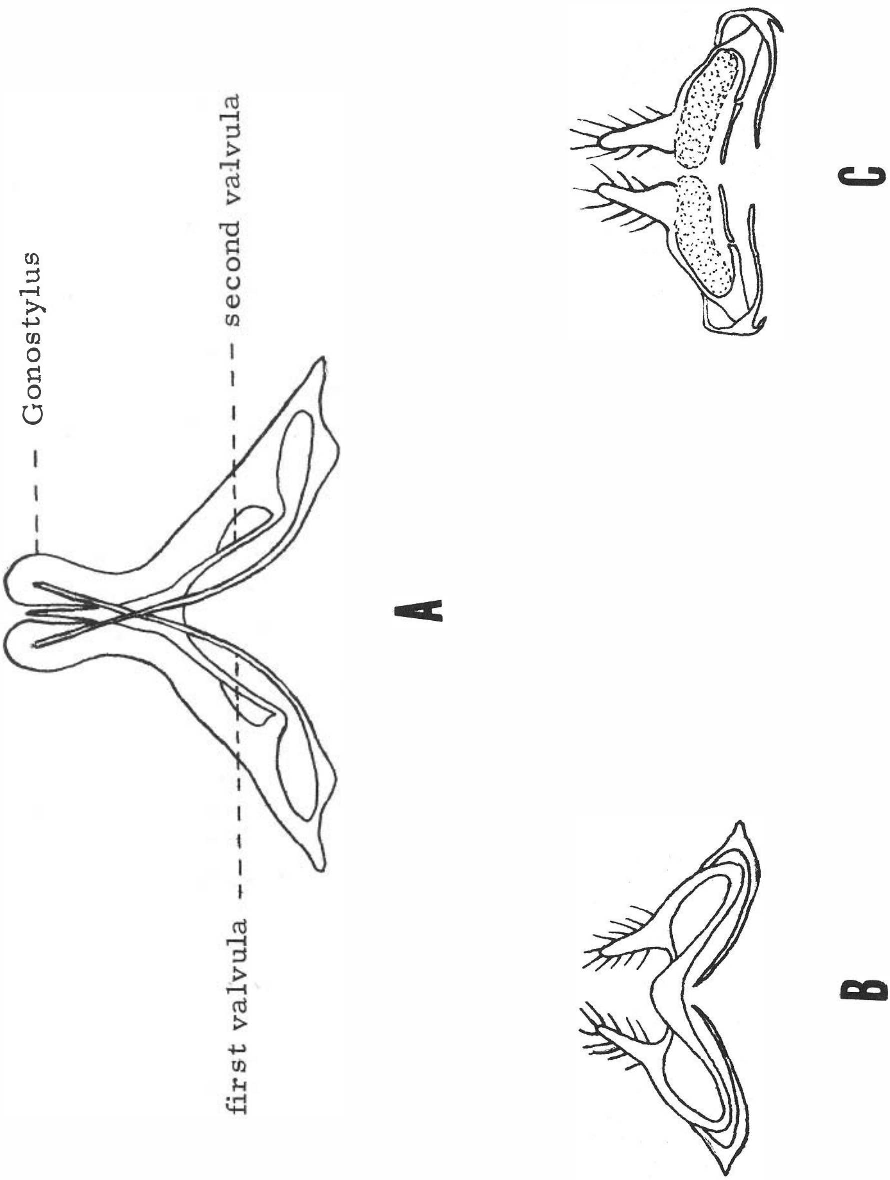

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Fig. 7: Phylogenetic tree showing the main evolutionary trends in the stingless bees.