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Phylogeny and relationships among the genera and subgenera of the stingless bees (Meliponinae) of the world

by

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Abstract: The present work attempts to establish probable evolutionary trends and relationships among the various groups of stingless bees, and in doing so to provide a new classification for the subfamily Meliponinae.

This study concludes that the stingless bees had their center of origin and dispersion in Africa. This is based on the wide acceptance of continental drift, the primitiveness of several African Meliponinae, and the discovery of a European stingless bee fossil from the late Eocene, which shows that the Meliponinae were not restricted to America at that time.

Parallel evolution seems to have taken place between the African genera and several groups of stingless bees from other continents. For instance, resemblances between *Cleptotrigona* and *Lestrimelitta;* between *Dactylurina* and *Tetragona;* between *Meliponula* and *Melipona;* and between *Meliplebeia* and *Plebeia,* result from parallelisms or convergences.

The new classification here presented demostrates and defends the recognition of certain groups as genera and subgenera, and the relegation of other names to synonymy.

The purposes of this paper are to indicate probable evolutionary trends and relationships among the various groups of stingless bees, and in doing so to provide a new classification for the subfamily Meliponinae. The study is based on characteristics of both biology and comparative morphology. Stingless bees are the only reasonably near relatives of the hive bee and its congeners of the genus *Apis,* as well as of the bumblebees (Bombini) and orchid bees (Euglossini).

They are widespread in the tropical regions of the world, although their greatest concentration and diversity are in the American tropics. They occur in colonies in which the female castes, queen and worker, are strikingly different morphologically; in this feature they resemble only *Apis,* among the bees. In size they range from workers larger than those of hive bees to minute forms, only 2 mm in length.

The entire morphological study was based on the worker caste. Queens are difficult to obtain and are poorly represented in collections. Although males of several species were available, they were not well enough represented to make their

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study worthwhile. Workers of a total of 160 species were studied. There remain, however, several species which I have not seen, but the species examined represent all the main morphologically and biologically recognized groups from all the areas where stingless bees occur, i.e., tropical America, Africa, Indo-Malaya and Australia.

Taxonomists who specialize on any given group may tend to use many genera or subgenera. Others, on the contrary, may have opposite tendencies, recognizing few taxonomic groups. In dealing with the stingless bees (Meliponinae) I intend to follow an intermediate course between the so called splitters and lumpers. In my opinion, among the Meliponinae there are important advantages, for instance, in retaining together in a single genus, *Trigona,* all members of the *Trigona* line except *Lestrimelitta* and the African groups, instead of breaking them down into some 32 genera as has been done (Moure, 1943, 1946, 1950, 1951, 1953, 1961). All these bees have essentially similar biologies, and they are similar in appearance and basic morphology, in spite of the differences which exist. In the broad sense here used, *Trigona* has a meaning to entomologists and biologists which it would lose if dismembered. I know of no comparable advantages that would result from division of the genus.

Although I appear to disagree with Moure's classification of the stingless bees, the difference between the present arrangement and that of Moure is largely a matter of classificatory levels. We are in general agreement as to the interrelations of the groups. Furthermore, the extreme splitting of Moure's scheme has served a useful purpose, namely, to demonstrate the existence of natural but minor phyletic lines. Moure has discovered a great number of useful external characters, most of which have been used in this work. He has also made a valuable contribution toward a general understanding of the phylogeny of this group.

Convergence is the nightmare of the taxonomist; this type of evolution results in similarities, sometimes many of them, and can affect detailed characters which nevertheless are not proof of cladistic relationship. Such characters are homoplastic or analogous and not homologous. Parallelism is even worse, mostly because the effects are still more difficult to distinguish from homology. However, close parallelism is by itself an indication of relationship. Some of the mistakes which have been made in the interpretation of phylogeny, and in consequence in the classification based on it, have been due to the confusion of convergence and homology. Therefore, one of the taxonomist's goals should be to discover and correct these mistakes. Unfortunately, this effort is not always easy, especially if good fossil evidence is lacking. Among the stingless bees, for instance, such evidence is meager, and it is easy to fall into certain mistakes of interpretation.

Parallelism, convergence and divergence can occur among groups of organisms evolving independently: they can undergo similar changes and continue to resemble each other; they can become more and more similar, or less and less similar. It is obvious that these names describe types of evolution but do not explain them. The characters found in the organisms which are evolving in a parallel, convergent, or divergent manner are usually related to the mode of life of the organisms involved, in other words, the characters are generally adaptive.

Although convergence and parallelism are difficult to deal with, one should be aware that they are not universal and are never fully completed. We do not know of any case in which two groups have evolved in exactly the same way in all characters. Divergence, on the other hand, is a very common event: the groups become less similar as time passes, and all the separate evolutionary lines diverge to some degree, even if in some aspects there are convergences or parallelisms.

Among separate lineages, divergence is universal; this is one of the reasons why numerical taxonomy can be useful when dealing with groups that lack convergent or parallel evolution. When dealing with relationships of groups like subgenera, genera, or higher taxa, numerical taxonomy may have, in my opinion, certain pitfalls. Characters are not weighted. In the stingless bees, for example, when using 50 or more features, most of them of poor phylogenetic importance, no distinctions are made between such features as the nature of the thoracic portion of the dorsal vessel, the position of ganglion 3, or the nature of the alimentary canal. As a result, one may end up with a peculiar classification, based largely upon apparently trivial characteristics, because they are frequently involved in parallelisms and convergences. This is well illustrated in the work of Blackith and Blackith (1968), who computerized taxonomic analyses of the relationships of the orthopteroid insects. The resulting conclusions are not acceptable to most specialists on Orthoptera; among other things, Dictyoptera are separated from the stalk of the Ensifera. For an excellent criticism of this subject see the recent article by Hubbell (1978), in a newsletter entitled Metaleptea, of the Pan American Acridological Society (PAAS).

In a recent work, Kerr and Cunha (1976) used numerical taxonomic techniques in an effort to determine the position of two fossil bees, originally described as *Meliponorytes devictus* Cockerell (Miocene, Burma) and *Electrapis proava* (Menge) (Oligocene, Baltic). They used 51 characters, all of which can be regarded as very superficial and of poor phylogenetic importance; as a matter of fact, all of them are used for the description of species. In other words, like most numerical taxonomists, they used characters not at the generic or subgeneric level, but rather at the specific level. Nevertheless, they were right in their conclusions about *Meliponorytes devictus,* which is very close to *Trigona (Tetragona) iridipennis;* they called it *T. (Tetragona) devicta.* On the other hand, they were quite wrong in relation to *Electrapis proava,* a bee which does not even belong to the Meliponinae (Wille, 1977; Winston and Michener, 1977).

The above comments could easily be interpreted as an attack on numerical taxonomy as such. This is far from the truth, the criticism being actually aimed at the people engaged in such endeavors. Numerical taxonomy presumably has a significant future, since its techniques are developing rapidly. Numerical taxonomists should soon be able to deal with convergent and parallel evolution. Among other things, they will be more aware of the importance that certain characters should have, and they also are bound to be more selective as to the criteria they use. The weighting of characters and the use of more significant traits, is, in my opinion, the critical point for the future of numerical taxonomy.

A final point should be made here. As we grow up we acquire knowledge about the world that surrounds us. Much of this knowledge we take as matter of fact, usually without questioning its real nature. This tendency manifests itself as preconceived ideas. Unfortunately scientists are no exception to this rule. Clearly this should not be so, but our general education and our cultural determinism impel even the best scientists to behave within a general framework. Perhaps this can be observed best by those working in taxonomy. It is still more evident when dealing with some hypothetical realms, such as the phylogenetic relationships of animal groups. A scientist, when working on this subject, usually enters this field with a series of preconceived ideas. These ideas seem to be the result of several things: 1) his own training and specialization; 2) his experiences and personal idiosyncrasies; 3) a subconscious desire to prove specific views, maybe because of professional rivalry; 4) acceptance of the views of his colleagues which appeal to him; and, 5) awareness of preconceived ideas among his colleagues, who have expressed them as almost sacred truths.

Actually there is nothing wrong in preconceived ideas, even in a scientific endeavour, providing that one is aware of this tendency in human behavior, and providing that they are not regarded as sacred truths. Otherwise a scientist may spend all his life just trying to prove his own views, which may happen to be wrong. In this case, no matter how hard he works he will never be able to contribute to the advancement of science.

MATERIAL AND METHODS

The introductory discussion is intended, in part, to lead up to the methods used in the present study. One of the major aims is to make use of all possible knowledge at hand about evolutionary tendencies found in well known groups of animals. To treat the Meliponinae ignoring completely all that we have learned about adaptive radiation and phylogeny in other groups would be, in my opinion, a mistake. We should take advantage of all the facts available concerning the evolutionary tendencies of other animals which have well documented fossil records, and when possible we should apply this knowledge, by analogy, to groups, like the Meliponinae with scanty fossil evidence. Indeed, Nature being always cyclical, carrying out her processes in a series of recurrent phases, it would be natural to make comparisons among different animal groups, since the general patterns seem to repeat themselves.

No plans were made to use numerical taxonomy in this study, partially because, like so many other zoologists, I have not been well trained in this field, and partially because of what has been said in the Introduction. I have used instead the more traditional method in which one rather intuitively recognizes natural groups on the basis of overall "phenetic" similarities, and then studies relationships of these groups. This is a common method in scientific endeavour, although it is not usually mentioned, perhaps because it is hard to define, or because most scientistst are afraid to admit it, or simply because they are not aware of it. When a scientist is able to use this method, whether consciously or unconsciously, it opens up for consideration much material and circumstantial evidence previously thought unworthy of attention. All this, of course, is no proof but a pointer toward proof. If the application of the scientific method is carried into the subjective realm, a rich and rewarding field of speculation becomes available and carries a conviction which no mere external proof can provide. Intuition, as used by scientists, is a combination of both the scientific approach and of inner feelings, in other words, the scientists are able to enter the subjective sphere, giving us their mental picture about the inside of things, in matters which the objective scientific method cannot touch.

Most, if not all, scientists realize that there is no final answer to their scientific problems, except for those which they find out for themselves; and that when they have found an explanation it will still not be final, because it always leaves further problems to be explored. Contrary to what one might think at first, the sense that everything is known that can be known, is frustrating and detrimental. This attribute is what makes a scientist dynamic and urges him to always expand the frontiers of his field of knowledge.

Most of the specimens used in this study belong to the Snow Entomological Museum of the University of Kansas. The specimens used in the study of internal morphology were preserved in Dietrich's (Kahle's) fixative and were collected by the author, mainly in Mexico and Costa Rica. Dissections were done under water, and usually more than one specimen was dissected for every species examined. For the study of internal skeletal structures, dry specimens were placed in alcohol for 24 hours and then dissected and cleaned under water; this method was found more practical than using potassium hydroxide.

A detailed description of the morphology of the stingless bees is not given here since it is already available in the literature (Camargo *et al.*, 1967). All possible available characters of the external and internal anatomy as well as the general biology have been carefully studied in an effort to interpret the variations within the Meliponinae.

SYSTEMATIC POSITION OF THE STINGLESS BEES AND A GENERAL CONSIDERATION OF THEIR PRIMITIVE AND DERIVED CHARACTERS

Systematic position and characterization: In a recent study Winston and Michener (1977) evaluated the morphology and the social behavior of stingless bees and honeybees. Very properly they concluded that highly eusocial behavior arose twice in the bees, suggesting an early differentiation and a strong divergence of the stingless bees from the remaining Apidae. This new view has now divided the family Apidae into three subfamilies: Meliponinae, Apinae, and Bombinae, the latter with the tribes Euglossini and Bombini.

The following features characterize the Meliponinae:

1. Wing venation reduced and weak; marginal cell relatively short, equal to or slightly larger than length of cell lst M, and apically open or faintly closed; submarginal cells absent, but sometimes first abscissa of Rs and first r-m cross vein weakly indicated; second m-cu cross vein absent, resulting in an open cell 2nd M.
2. Pterostigma of moderate to large size, extending well beyond base of vein r. Hamuli few.
3. Jugal lobe of hind wing more or less half as long as vannal lobe; jugal incision normal, not minute.
4. With penicillum, a brush-like group of long stiff setae located anteriorly on outer apical margin of hind tibia. This structure is unique to the Meliponinae; it is absent or weak, however, in *Hypotrigona,* and parasitic genera *(Lestrimelitta* and *Cleptotrigona)*
5. Rastellum usually well developed, except in *Axestotrigona, Meliplebeia, Hypotrigona, Trigonisca, Meliponula*, and parasitic genera.
6. Without an auricle for pressing pollen upward into the corbicula.
7. With a relatively small and slender hind basitarsus, like that of most other bees.
8. Maxilla with a well developed process which extends from the basal end of the stipes to the submentum. This process is lost, according to Winston and Michener (1977), in other apids.

9. Maxillary palpi absent.

10. Subgaleal sclerite heavily sclerotized and with a strong triangular projection at each end.

11. Posterior border of supraneural bridge of prothoracic endosternum (apophyseal arms) notched at midline, resulting in a bilobed posterior border, with lobes usually rounded (Fig. 27). Apohyseal arms usually separated (Fig. 28), but in some fused along midline *(Meliplebeia, Cleptotrigona, Axestotrigona, Scaura, Oxytrigona, Lepidotrigona)* Fig. 27.

12. Wax glands dorsal.

13. Tergal and sternal apodemes reduced.

14. Hind tibial spurs lacking; claws of female simple.

15. Sting reduced.

In general, the stingless bees are easily distinguished from other bees by the reduction and weakness of the wing venation, by the presence of a penicillum in the hind tibia, and by the reduction of the sting.

Tribes of Meliponinae: In 1961 Moure divided the stingless bees into the tribes Meliponini and Trigonini. A few years before, the gap between these two groups was apparently smaller than that normally found between tribes (e.g., in those recognized by Michener, 1944). The narrowness of this gap was further supported by the difficulty many investigators encountered for almost a century in separating *Melipona* and *Trigona s. lat.* In more recent years, however, the separation of these two groups has been made easier by the discovery of a series of apparently valid taxonomic characters, such as those concerned with the general biology and nest architecture (many authors), the dorsal vessel (Wille, 1958), the ventral nerve cord (Wille, 1961), and the alimentary canal (Cruz-Landim and Rodríguez, 1967). It is now obvious that there has been strong divergence of these two groups. Therefore it is reasonable to recognize two tribes among the stingless bees: the Meliponini and the Trigonini. The differences are enumerated in Table 1.

Primitive and derived characters: In order to learn whether certain characters in a group studied are primitive or derived, it is usually important to know the state of the homologous characters in the group ancestral to the taxon under consideration. Since the ancestors of the Meliponinae are presumably extinct and not known, it was necessary to determine the generalized characters of the stingless bees by comparing all the characters studied with those of other bee groups. In general, any character found to be widely distributed among the stingless bees, and among other groups of bees, was considered to be primitive in the Miliponinae. With this criterion in mind and using fossil evidence to help determine the most primitive stingless bee, one is also able to evaluate certain difficult characters. One is a flat gonostylus, found in most of the groups of African stingless bees. This character is usually associated with a better developed sting. It happens also that

TABLE 1

Characters differentiating the tribes Trigonini and Meliponini

Characters	Trigonini	Meliponini
Size	Usually small, 2 to 8 mm in length and slender	Usually rather large (from 8 to 15 mm in length) and robust.
Pubescense	Short and sparse, dense in *Meliponula*	Upper half of head and thorax densely hairy, hairs long
Length of fore wing	Usually long and extending well beyond apex of abdomen	Relatively short and not, or slightly, surpassing tip of abdomen
Pterostigma	Relatively broad, and distinctly rounded or convex below	Poorly developed, narrow to linear, not rounded below
Hamuli	Usually from 5 to 8*	From 9 to 16
Dorsal vessel	Thoracic portion straight, except in *Meliponula,* Fig. 4	Thoracic portion making an arch between longitudinal muscles of thorax, Fig. 5
Nerve system	Abdominal ganglion 3 located in first metasomal segment, Fig. 1	Abdominal ganglion 3 located in thorax Figs. 2,3
Alimentary canal	With a short digestive tract**	With a long digestive tract
Nature of the nest entrance and batumen plates	Usually made of cerumen	Usually made of mud. Nest entrance often with radial striations on outside surface
Royal cells	Nest with specialized queen cells, larger than those of workers and males	Nest without specialized queen cells
Location of queen cells	Usually found near periphery of combs or in the outer parts of cell clusters	Intermingled in the combs with cells of workers and males
Size of virgin queens	Larger than workers, thorax notably wider	Smaller than workers, thorax not notably wider
Ovaries of the newly emerged queens	Well developed	Undeveloped
Rate of production of queen	Relatively rarely produced	Frequently produced
Determination of workers and queens	Presumably trophically determined	Supposedly trophically and genetically determined

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* Except in *Meliponula, Trigona thoracica* and *T. capitata* in which there are 9.

** In *Trigona* the shortening is due to the reduced length of the hind gut, while in *Lestrimelitta* the shortening is due to the reduction of both ventriculus and hind gut (Cruz-Landim and Rodríguez, 1967).

most of these African groups are primitive in many other features, like the absence or weakness of the rastellum. Hence a flat gonostylus is regarded here as a primitive character. A weak rastellum consists of long, slender, tapering hairs, curved and presumably quite flexible. When the rastellum is absent, there are only plumose hairs along the apex of the inner surface of the hind tibia. The rastellum is absent only in *Axestotrigona* and some *Hypotrigona* and *Meliplebeia**. It is weak in *Meliponula, Trigonisca,* and most *Hypotrigona* and *Meliplebeia.* The lack of or a weak rastellum is regarded here as primitive; without a functional rastellum a bee has no way to tranfer pollen that lodges on the abdomen to the corbicula. It seems unlikely that any nonparasitic bee would lose the ability to do this, and it is significant that bees without a functional rastellum belong to African groups (except *Trigonisca*) with relatively primitive stings. On such bases a list of characters believed to be primitive was made, as well as another list, representing the conditions derived from the primitive ones (Table 2). Of course any of these primitive characters may be retained by certain specialized forms. The places of appearance of specialized characters in the cladogram are shown in Figure 30.

The primitive characters listed in Table 2 are regarded as the major features that should characterize species near the base of the trunk of any phylogenetic tree for the Meliponinae. The other features, those listed under "derived character", are mostly specialized attributes found in specific genera and subgenera. Sometimes two or more derived conditions may have arisen from a single primitive one, and intermediate types often occur. One of these cases is shown in Table 2, by characters listed under (12a), (12b), (12c), and (12d)**. A trend of the inner side of the hind tibia is to evolve a bare, posterior, depressed rim which tends to become wider. The first step is a very narrow rim (12a); the last step is a very broad rim, with a silvery pilose median elevation along the inner side of the tibia (12c). Character (12b) is intermediate. Feature (12d) is like the primitive character, but because of association with other features, it is believed to be a reversion.

To evaluate the levels of specialization among different groups of Meliponinae, a relative value has also been given in Table 2 for each derived character. Three categories were recognized: a) when a character has arisen independently among three or more groups of stingless bees, the value given is 1, 16 characters belong in this category, b) when a character is found only among one or two groups, the value is either 2 or 3 (3 was used when a feature appeared more important than value 2), 17 characters fall in this category; c) when the character is unique, very specialized, and found only in one group, the value given is 4. Only two unique features were placed in this category: the location of abdominal ganglion 3 in the thorax, found in *Melipona,* and brood cells arranged in vertical combs, found in *Dactylurina.* Values 2 and 3 of the second category may appear as relative and subjective; however, any changes between values 2 and 3 that others may make would not much alter the general picture of levels of specialization of the different groups of Meliponinae.

Some apparently good primitive characters were not included in Table 2, such as the cluster type of arrangement of brood cells, and the lower chromosome

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* Very likely the rastella were secondarily lost in the parasitic groups, *Cleptotrigona* and *Lestrimelitta,* or at least in the latter.

** In order to indicate any derived character, the number of the structure is placed in parentheses.

number. The reason for these omissions is that these features are not found in the most primitive genera; they are found in several groups of Meliponinae, including both primitive and specialized subgenera. For example, in the subgenera *Plebeia, Scaura, Partamona,* and *Tetragona* one is able to find brood cells arranged both in clusters and in combs, while in *Axestotrigona* and *Meliplebeia,* regarded here as the most primitive genera, one finds only combs, (Wille and Michener, 1973). Chromosome data are known for 27 species of stingless bees, and according to Kerr (1969) polyploidy in Meliponinae seems evident in two groups: Trigonini with *Trigona muelleri* n=8, several others with n=15, 17, and 18; and Meliponini with *Melipona marginata* (and other *Melipona* species) n=19, while *Melipona quinquefasciata* is n = 18. Size and yellow maculations are other interesting features since several known fossil stingless bees are very small and with yellow maculations.

Although they may actually represent primitive conditions, these features were not included in Table 2 for the reasons discussed above. For example, very small size is not found in either *Axestotrigona* or *Meliplebeia,* and melanic forms are found in several species of stingless bees with yellow maculations.

TABLE 2

*Primitive characters and derived alternatives in stingless bees**

	Primitive character	Derived character	Relative Value
1.	Abdominal ganglion 3 located in first metasomal segment, Fig. 1	Abdominal ganglion 3 located in thorax *(Melipona)* Figs. 2,3	4
2.	Dorsal vessel with thoracic portion straight, Fig. 4	Dorsal vessel with thoracic portion making an arch between longitudinal muscles of thorax *(Melipona* and *Meliponula),* Fig. 5	3
3.	Short digestive tract due to reduced length of hind gut (investigated only in 13 species)	Long digestive tract due to length of the hind gut *(Melipona)*	3
4.	Gonostylus flat *(Axestotrigona, Meliplebeia, Cleptotrigona, Meliponula, African Plebeia* and *Dactylurina),* Figs. 6,7	Gonostylus cylindrical and pointed or small and tuberculiform, as in *Partamona,* Fig. 8	1
5.	Sting structures relatively well developed, but very short *(Axestotrigona, Meliplebeia* and *Meliponula)* Fig. 6	Sting structures vestigial (in most stingless bees), Fig.8	1
6.	Penicillum present, hairs stiff	Penicillum vestigial or absent (*Hypotrigona,* and parasitic bees *Cleptotrigona* and *Lestrimelitta)*	1

	Primitive character	Derived character	Relative Value
7.	Rastellum weak or absent (*Axestotrigona, Meliplebeia, Meliponula, Hypotrigona,* and *Trigonisca)*	Rastellum present, hairs stiff (Rastellum probably secondarily lost in the parasitic *Lestrimelitta* and perhaps *Cleptotrigona*)	1
8.	Proboscidial fossa slightly narrow posteriorly, Fig. 9	Proboscidial fossa very narrow posteriorly *(Cleptotrigona* and *Lestrimelitta)* Fig. 10	2
9.	Cuticular surface smooth with punctation sparse and delicate	Cuticular surface coarsely pitted on the head and thorax *(Nannotrigona)*	3
10.	Pilosity of thorax sparse	Pilosity of thorax dense *(Meliponula* and *Melipona*)	2
11.	Mandibles bidentate on inner apical margin, Fig. 12	a. Mandibles unidentate *(Cephalotrigona* and *Dactylurina)* Fig.11.	2
		b. Mandibles quatridentate or quinquedentate (Paratrigona and *Trigona)*. Figs. 13,14.	
12.	Inner side of hind tibia without a depressed area at the posterior rim (*Axestotrigona*) (See derived character d)	a. Inner surface of hind tibia with a very narrow bare posterior depressed *(Plebeia, Scaura, Meliplebeia* and *Meliponula)*, Fig. 15.	1
		b. Inner side of hind tibia with a relatively narrow bare posterior depressed rim (Much wider than in a) *(Hypotrigona, Trigonisca,* and *Oxytrigona)*, Fig. 16.	1
		c. Inner side of hind tibia with a silvery pilose median elevation that extends along the whole length leaving a relatively broad, flat and practically bare posterior zone depressed *(Cephalotrigona, Lepidotrigona, Tetragona, Trigona,* and *Dactylurina)*, Fig. 17.	1
		d. Depressed area lost *(Nogueirapis, Paratrigona, Partamona, Scaptotrigona, Nannotrigona, Melipona,* and parasitic bees *Cleptotrigona* and *Lestrimelitta)*, like the primitive character, but because of association with other characters, believed to be reversions.	1

	Primitive character	Derived character	Relative Value
13.	Hind tibia more or less claviform to triangular	Hind tibia spoon-shaped (*Axestotrigona, Partamona* and *Lepidotrigona*), Fig. 18	1
14.	Hind tibia without posterior parapenicillum; at most some hairs located anteriorly and close to the penicillum (as in *Trigonisca*)	Hind tibia with posterior parapenicillum (*Scaptotrigona, Partamona, Nannotrigona, Cephalotrigona, Lepidotrigona, Scaura, Tetragona, Trigona,* and *Meliponula*), Fig. 20	1
15.	Hind tibia without anterior parapenicillum	Hind tibia with anterior parapenicillum (*Meliponula*), Fig. 20	1
16.	Posterior lateral margin of hind tibia with simple hairs only	Posterior lateral margin of hind tibia with simple and plumose hairs (*Tetragona, Trigona* and *Dactylurina*)	1
17.	Corbicula present	Corbicula lost. (The parasitic bees, *Cleptotrigona* and *Lestrimelitta*)	1
18.	Hind basitarsus relatively small and flat	Hind basitarsus strikingly large and swollen (*Scaura*), Fig. 19	2
19.	Inner surface of hind basitarsus uniformily covered with bristles	Inner surface of hind basitarsus with a suboval, bristleless, sericeous area just below the neck or upper part (*Trigona* and most species of Oriental *Tetragona* and four species of American *Tetragona*)	1
20.	Midgut of moderate length	Midgut short (*Lestrimelitta*)	3
21.	Lateral portions of epistomal suture straight or slightly curved throughout, and diverging anteriorly, Fig. 21	Lateral portions of epistomal suture subparallel in upper halves or more, and abruptly divergent in lower halves (*Trigona* and *Partamona*), Fig. 22	2
22.	Mesoscutellum without median basal fovea	Mesoscutellum with median basal fovea or V-or U-shaped depression (*Scaptotrigona* and *Nannotrigona*)	3
23.	Mesoscutellum relatively short	Mesoscutellum extending backward over propodeum (*Nannotrigona,* several species of *Paratrigona* and few *Tetragona*)	1
24.	Borders of mesonotum without scale-like hairs	Scale-like hairs bordering mesonotum and sometimes scutellum (*Lepidotrigona* and one *Tetragona*)	1
25.	Apex of mesoscutellum rounded	Apex of mesoscutellum notched (*Nannotrigona*)	2

	Primitive character	Derived character	Relative Value
26.	Marginal vein (Rs) slightly arched basally	Marginal vein strongly arched basally *(Trigonisca)*, Fig. 23	2
27.	Abdomen relatively short and wide, with first metasomal segment wider than long	Abdomen very narrow and claviform with first metasomal segment longer than wide *(Dactylurina)*	3
28.	Brood cells arranged in clusters or horizontal combs	Brood cells arranged in vertical combs *(Dactylurina)*	4
29.	Queens relatively rarely produced	Queens frequently produced *(Melipona)*	2
30.	Virgin queens larger than workers, raised in specialized royal cells, larger than those for workers and males	Virgin queens subequal in size to workers, raised in normal cells *(Melipona)*	2
31.	Ovaries of the newly emerged queens well developed	Ovaries of the newly emerged queens not developed *(Melipona)*	2
32.	Secretion of mandibular glands not poisonous	Secretion of mandibular glands poisonous *(Oxytrigona)*	3

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* Since only the genus *Trigona s. lat.* is regarded here as composed of several subgenera, the name *Trigona* as used in Table 2 means the subgenus *Trigona s. str*. The same practice is followed in the rest of the paper except where the generic meaning is indicated.

SPECIALIZED CHARACTERS AMONG THE MELIPONINAE

An important specialized feature of the Meliponinae is the reduction of the sting. As is well known, the sting is a derivation of the ovipositor of the Hymenoptera, in which we can find three adaptive stages: 1) as ovipositor among the primitive families; 2) as an instrument to paralyze or kill prey, as is the case of many wasps, and 3) as a defense mechanism, especially among the social species of the order. In some groups of social Hymenoptera the sting is not the only defense, and is frequently reduced or lost.

For instance, among ants there are two subfamilies, Dolichoderinae and Formicinae without stings; they defend themselves by biting, by spraying venom or by other means. Among primitively eusocial colonies, such as those of the tribe Halictini, as well as in some species of Augochlorini and the allodopine group, defense through the use of a sting is not important. This is perhaps due to their small size, and because they do not store great amounts of food. On the other hand, in those social bees that are of large size, such as the primitively eusocial bumble bees and the highly eusocial honeybees, the effectiveness of the sting is well known.

One possible explanation of this correlation between effective sting defense and large size may stem from the fact that the frequent predators against these colonies are relatively large animals. Stings by small bees would merely tickle large animals.

A possible secondary evolutionary trend, due to the lack of a functional sting in the Meliponinae, could be the cephalization of the ventral nerve cord. This view is reinforced by the fact that among the males of all bees there is a tendency toward reduction of the number of ganglia, which, according to Cruz Landim *et al.* (1972), is due to the absence of the sting in the male. On the other hand, in Meliponinae, the workers as well as the males have, in general, the same number of ganglia.

The trend toward cephalization of the ventral nerve cord occurs only in *Melipona* (Wille, 1961, Fig. 1). Here the abdominal ganglia migrate from two to four segments forward from their proper segmental positions. As a result, ganglion 3, which in primitive bees was located in the second abdominal segment (first metasomal segment), has moved well inside the thorax. The presence of ganglion 3 in the thorax is characteristic of all the species of *Melipona.* The greatest cephalization is found only in a few species, such as *Melipona nigra (=flavipennis)* (Wille, 1961), and *M. quadrifasciata* (Cruz Landim *et al.*, 1972), in which ganglia 4 and 5 have moved into the second abdominal segment, and ganglia 6 and 7 into the third (Fig. 3). Therefore the cord extends posteriorly only as far as the third abdominal segment, *i.e.*, the second metasomal segment (see Wille, 1961, Fig. 2, E). There are, of course, intermediate types. Ganglion 3 is found in the thorax only in *Melipona*, Bombini and Euglossini (Dias, 1958; Cruz Landim *et al.*, 1972), perhaps a good example of parallel evolution.

It is very significant that all the fossil forms of stingless bees known are very small, and therefore the first Meliponinae were apparently minute bees. This trait could be the key to their general evolution, and to the significance of certain specialized characters. For instance, the reduction of the wing venation may be a result of small size of the bee, since small fragile insects do not need strong veins in their wings for efficient flight. Among the Hymenoptera good examples of this characteristic are the wasps of the superfamily Chalcidoidea and several unrelated genera of minute bees, such as some species of Euryglossinae (Colletidae), *Perdita* (Andrenidae), and the genera *Neolarra* and *Parammobatodes* (Anthophoridae).

One possible advantage of being big, at least among the Meliponinae, could be to discourage predators. The smallest *Trigona* are fair game for the most abundant insectivores, such as the small *Anolis* lizards, numerous in the American tropical rain forest. Another reason for becoming bigger, might have been that the larger the bee, the larger the flight range becomes, which means better exploitation of food sources. Size could bring a new degree of freedom. Big stingless bees fly more widely and spend more time out of their nests, partly because they have less to fear and partly because they need more food and have to travel farther for it. In other words, they have encountered a wider and more varied environment. There may be other possible reasons for the trend toward larger size, such as avoiding competition with smaller species, or perhaps even self-defense against smaller stingless bees.

As many species of stingless bees became moderate-sized, the already reduced wing venation may have become at the same time a disadvantage, and perhaps a limiting factor against becoming very large. The relatively big pterostigma of the fore wing of most Meliponinae probably counters fragility of the wings. Yet it is interesting to remember that the smallest stingless bees *(Trigonisca* and *Hypotrigona)* have relatively larger pterostigmata, while the bigger meliponines (e.g *Melipona*) have relatively smaller pterostigmata, actually poorly developed. The

Melipona, however, have a further modification of their wings: contrary to other stingless bees, their wings are relatively short, usually not reaching the tip of the abdomen or at most extending only slightly beyond it. The number of hamuli of the hind wing is also correlated with the size of the bees. The number ordinarily varies from 5 to 14. In *Meliponula* and *Melipona,* which are the largest stingless bees, the number is from 9 to 14 (occasional specimens may have 8 or more than 14; *Meliponula* and the smallest *Melipona* have 9). The remaining groups have less than 9 hamuli (usually 5 to 8) per hind wing.

In *Melipona* (Wille, 1958) and in *Meliponula* (Wille, 1963) the thoracic portion of the dorsal vessel forms an arch between the longitudinal muscles, and before entering the space between the muscles, it makes a small loop in the posterior portion of the thorax, called the thoracic loop (less evident in *Meliponula*). The entrance between the longitudinal muscles is close to the anterior ventral border of the second phragma, and the ascending portion lies along its midline. Then there is a horizontal portion, which runs along and in the middle of the longitudinal dorsal muscles of the mesothorax. The descending section is well differentiated from the horizontal portion in *Melipona,* but in *Meliponula* the descending portion slopes gently and is not well differentiated from the horizontal one. There is also a loop in the first metasomal segment before entering the thorax and another smaller loop, less marked in *Meliponula,* between the second phragma and the propodeum (Fig.5). In all the other genera and subgenera of Meliponinae the thoracic portion of the dorsal vessel is straight, running along and dorsal to the gut, and never between the longitudinal thoracic muscles. This arrangement we can call Type 1, and that of *Melipona* and *Meliponula* Type 2. The comparative study of the dorsal vessels of Apoidea suggests that Type 1 is primitive, while Type 2 is derived (Wille, 1958). Actually in any family or tribe in which both types are found, Type 1 is always present among the more primitive forms. Another important conclusion that one can draw from the comparative study of dorsal vessels of apoids and which was not considered in the previous work, is that most bees with a Type 1 vessel are slender and weak, like the Paracolletini, Hylaeinae, Halictinae, Dufoureinae, Andrenidae, Exomalopsini (except *Monoeca*), Nomadinae *(Nomada, Neopasites, Tripeolus)*, Ceratinini, and *Trigona.* On the other hand, bees with dorsal vessels of Type 2, tend to be more robust and larger (at least relative to the members of the same family or tribe), such as the Colletini, Diphaglossinae, Nomiinae, Oxaeidae, most Megachilidae, Eucerini, Melitomini (=Emphorini), Anthophorini, Centridini, Xylocopini, Bombini, Euglossini, Apinae, *Melipona* and *Meliponula.* Among the most robust and largest of all bees, *Xylocopa,* the thoracic portion of the dorsal vessel is the most complex (Wille, 1958, Fig. 17). The ascending portion, for instance, almost reaches the notum, and the descending section forms a large loop. All this seems to suggest a correlation between bees with apparently more effective flight mechanisms, and therefore with stronger thoracic muscles, and dorsal vessels of Type 2. One possible explanation is that those bees with stronger flight mechanisms may need more effective blood irrigation in the thorax.

In the head, the vessel opens just behind the brain, between the corpora allata. When the longitudinal muscles are contracted, the second phragma is pulled forward and, because the ascending portion of the vessel lies along the midline of the phragma, that part of the vessel should also be pushed forward. It is likewise possible that the contraction of the thoracic muscles may squeeze the aorta, and thus help in impelling the blood forward in a more effective way and therefore enhance irrigation of the head and thorax, which could be advantageous when there is a great deal of muscle activity.

Although there are many specialized characters in the stingless bees where functional significance can be inferred, there are also many features where this significance is not evident. Among them are the median elevation on the inner surface of the hind tibia and the bristleless sericeous area on the hind basitarsus.

Among the minor traits which are possible to interpret are the following concerning the penicillum and the coarse hairs on the thoracic venter and coxae: based on observation of *Trigona pallida,* Winston and Michener (1977) reached the following conclusion "Stingless bees transfer pollen from the middle leg to the hind leg of the same side by pulling the former through the space between the penicillum and the base of the hind basitarsus. Because of the curvature of the penicillum, such a movement apparently pushes pollen up into the corbicula". Other observations (Michener, Winston and Jander, 1978) on *Trigona* show that pollen gathered by the fore basitarsi is brushed off into backward-directed hairs of the thoracic venter, whence it is picked up probably by the middle legs for transfer to the hind legs.

The parapenicillum is a row of long, curved bristles located just anterior of the penicillum; these structures are very similar although the former is somewhat smaller. I have seen specimens of *Scaptotrigona* with pollen between the parapenicillum and penicillum. It is probable that the parapenicillum helps the penicillum in its function.

A posterior parapenicillum is found only in *Meliponula bocandei,* and it is apparent that it functions in helping to hold in place a large pollen mass on the corbicula. The hind tibia in *Meliponula* is a very strong, with the distal two fifths concave and shiny (corbicula), while the upper three fifths are convex, dull and finely granulose. It seems that the hind tibia is built to hold a large pollen mass only in the lower or distal two fifths and that a posterior parapenicillum helps to support it (Fig. 20).

The long, dense, simple and plumose hairs, along the posterior border of the hind tibia of the subgenera *Trigona* and *Tetragona* serve to hold large masses of pollen or other materials being carried to the nest. It is perhaps significant that it is among these subgenera that the largest colony sizes have been recorded.

The bent or hooked condition of the dorsal hairs of the labium and maxilla of several stingless bees, such as *Dactylurina* and species of the subgenera *Trigona, Nannotrigona, Lepidotrigona,* and some species of *Tetragona,* may assist the mouth parts in pulling pollen from the anthers or from flowers with small tubular corollas.

ORIGEN AND DISPERSION OF THE MELIPONINAE AND THE PHYLOGENETIC SIGNIFICANCE OF THE AFRICAN STINGLESS BEES

Area of origin: If we take into consideration some relevant evidence we are faced with the conclusion that the Meliponinae had its center of origin and dispersion in Africa. There are three major and significant factors which show that Africa could be the center of origin of the stingless bees: 1) The wide acceptance of plate tectonics or continental drift; 2) The new fossil findings such as a stingless bee from the Baltic amber of the late Eocene; 3) The primitiveness of several African Meliponinae (Africa is the only place where some of the stingless bees have a better developed sting than the majority of groups).

Reyment (1969) has stated that, although the separation of South America and Africa was completed during the lower Createaceous, significant continental drift did not occur until the lower Turonian (some 95 million years ago). On the other hand, according to Veevers *et al.* (1971)*and Raven and Axelrod (1972)*, drifting took place during the mid-Cretaceous (approximately 115-110 million years ago). By the Cretaceous-Tertiary boundary (some 65 million years ago), South America had moved westward well away from Africa. At this time the east coast of North America and the west coast of Europe were presumably still in contact. Since Central America did not exist at this time, South America was a large isolated continent, which was separated from the Antartic by a narrow sea.

Kerr and Maule (1964) considered South America as the center of origin and dispersion of Meliponinae, mainly because that area now has the greatest number of species as compared with the Old World tropics. If we assume that the origin of the stingless bees probably took place at about the Cretaceous-Tertiary boundary and if we regard the above geological interpretations as true, then these bees did not originate in South America and disperse thence to Africa. The recent discovery of European fossils from the early Tertiary period (late Eocene), described by Kelner-Pillault (1970) as *Trigona eocenica,* showed that Meliponinae were not restricted to America at that time. Although she assigned this species to the subgenus *Hypotrigona,* there is still doubt as to its real taxonomic position (Wille, 1977). The finding of this stingless bee in Europe in the late Eocene** makes the theory of South America as the center of origin difficult to accept since South America was completely isolated, after separation from Africa, until the Pliocene, when a connecting bridge between North and South America was established. Before that the southern continent was disconnected from the northern by a relatively wide sea, with several small islands between. Although there is some evidence that some animals (Hystricomorpha rodents and Platyrrhini primates) were able to cross the sea between North and South America (Simpson, 1964)† it is, according to Kerr and Maule (1964), a well known fact that stingless bees do not fly over great water barriers. The swarming method used by the stingless bees limits their range to some 300 meters from the hive, because of a strong connection between mother and daughter nests, which can last up to six months (Wille and Orozco, 1974). For this reason, migration of Meliponinae is dependent mainly on land connections.

If we accept that the Meliponinae had its center of origin and dispersion in Africa, then the presence of a stingless bee in Europe in the early Tertiary could be easily explained, since the forced conclusion is that the Meliponinae migrated first to the north, possibly during the Eocene, when tropical moist climates had wide development. Since Europe was presumably still in contact with North America, these bees probably soon migrated to that continent, as well as to Asia.

Although Africa has at present comparatively few Meliponinae species (about 35), it is possible that during the early Tertiary the number of species was rather high. The number may have been greatly reduced by late Tertiary aridity in which

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* Cited by Langenheim and Lee (1974)

** The Paleocene is not mentioned in this work because is is not well represented in the Old World.

† According to some authors, however, the immediate hystricomorph ancestors of the South American types were not North American. The Old World and the South American monkeys are derived from a more primitive primate stock, with their resemblance being matters of convergence.

the Kalahari desert covered Angola and almost reached the Congo river, and the Sahara was also enlarged considerably.

Obviously, the Meliponinae found in South and Central America environmental conditions more favorable for speciation than in Africa. Spreading over a whole continent with highly varied environments, the stingless bees speciated profusely. Different lines became adapted to many ecological roles. They underwent, in short, an adaptive radiation on a grand scale. This is supported by the fact that in the Neotropical region there is more diversityof groups,a greater number of species (over 200), and the most highly specialized group, *Melipona.*

Of general interest is the evolutionary historyof the leguminous trees of the genus *Hymenaea,* from which the neotropical amber was produced and where fossil specimens of stingless bees were embedded. As was probably the case of the stingless bees, the genus *Hymenaea* originated in Africa in the early Tertiary (Langenheim and Lee, 1974) and then migrated to South and Central America, Mexico, and the West Indies when Africa and South America were close together. As in the case of Meliponinae, *Hymenaea* found in the neotropical region an ideal place for speciation. At the present time, 16 species of *Hymenaea* occur in the tropics of the New World, while in Africa only one form is known, *H. verrucosa.* This species is now confined to the eastern part of Africa (coastal Kenya, Tanzania, and Mozambique) and to the island of Zanzibar, the Seychelles, Madagascar, and Mauritius. Langenheim and Lee (1974) suggest that there was a common West African ancestral stock for the neotropical species of *Hymenaea,* as well as for the primitive African form, *H. verrucosa.* The near extinction of *Hymenaea* from Africa was possibly due to the Pliocene drought. New geological evidence also indicates that during the Middle Pleistocene, aridity reduced the Congo rainforest, and the West African forest was fragmented some 22,000 years ago (Moreau, 1966) *.

The other relevant evidence that Africa was the center of origin and dispersion of Meliponinae is that in this continent are found the most primitive of all the stingless bees. The two groups with the minimum of specialized characters, *Axestotrigona* and *Meliplebeia,* are African groups. Furthermore, Africa is the only known place where some stingless bees have a better developed sting, resulting from fusion of the second valvulae into a short stylet and the first valvulae forming short lancets (Fig.6). A flat gonostylus, which has also been shown to be a primitive character, is also found only in the African species.

Phylogenetic significance of the African Meliponinae: If Africa was the place of origin and dispersion of the stingless bees, then the groups of that continent are implicitly of phylogenetic significance. We have already shown that the two most primitive groups of Meliponinae belong to Africa. However, there is another point of great phylogenetic significance, ignored until now, between the African stingless bees and those of other tropical areas. A careful study of the African groups shows that there is an interesting and instructive story of evolution and parallelism. I have pointed out before that most African groups represent subgenera of *Trigona,* with the exception of *Meliponula* (Wille, 1963). Even *Dactylurina,* although given generic status because of its specializations, was always thought to be a very specialized branch of the *Tetragona* group. It was not until making a phylogenetic tree of the Meliponinae that I realized the mistake: I had placed the *Dactylurina* line as coming off the base of the *Tetragona* and *Trigona* lines. At that time I

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* As cited by Langenheim and Lee (1974)

completely forgot that *Dactylurina* had a flat gonostylus, and it was assumed that the major line which gave origin to *Hypotrigona, Trigonisca, Oxytrigona, Cephalotrigona, Lepidotrigona, Trigona, Tetragona* and *Dactylurina* has a cylindrical gonostylus as one of the derived characters. Since *Dactylurina* has a flat gonostylus, it was obvious that it did not belong to that major line. It was then that I realized that the resemblance between *Dactylurina* and *Tetragona* is the result of parallel evolution. Soon after that, all the African groups with a flat gonostylus appeared to me as other cases of parallel evolution. There is parallelism between *Lestrimelitta* and *Cleptotrigona,* between *Melipona* and *Meliponula.* To some extent there is also some parallelism between *Partamona* and *Axestotrigona,* and between *Plebeia* and *Meliplebeia* (*Plebeiella* and *Apotrigona* are included in *Meliplebeia*). In all these cases the groups acquired similar characteristics independently of one another, but one should be aware that all of them stemmed from related ancestral stocks.

Parasitic life often results in convergence or parallel evolution; among bees we can even predict some common modifications of structure, like the disappearance of the scopa or corbicula in the females, and in the case of Apidae, the loss of penicillum, rastellum and auricle. I believe now that *Lestrimelitta* and *Cleptotrigona* are a good case of parallel evolution due to parasitic life. What we call here parasitic life means that survival depends on robbing other colonies for food and other materials. The presence of a flat gonostylus in *Cleptotrigona* indicated that this group arose from African *Trigona* with a flat gonostylus, while *Lestrimelitta* arose from Neotropical *Trigona* with a cylindrical gonostylus.

A flat gonostylus and a more developed sting than in other Meliponinae are found only in the African Meliponinae; all groups except *Hypotrigona* show these features. Since the present data suggest that Africa was the place of origin of the stingless bees, the presence of a flat gonostylus and a better developed sting in the African groups supports the hypothesis that these structures are primitive in the Meliponinae. Both structures have been retained in *Axestotrigona, Meliplebeia* and *Meliponula;* only a flat gonostylus is retained in the African *Plebeia, Cleptotrigona* and *Dactylurina.* Of all these African stingless bees, *Axestotrigona* and *Meliplebeia,* are the most primitive, while *Cleptotrigona, Meliponula* and *Dactylurina* are more specialized (see Table 3).

Assuming that *Lestrimelitta* and *Cleptotrigona* evolved by convergence, then the following features were acquired independently of one another: 1) Head relatively large, with vertex and gena very broad, proboscidial fossa very narrow posteriorly, postgenae forming two carinae which nearly meet to produce a postgenal bridge; 2) Small eyes; 3) Clypeus very small, width slightly more than three times its length; 4) Labrum with two protuberances laterally placed on outer surface, giving the structure a concave appearance; 5) Scutellum relatively short leaving a great portion of the metanotum uncovered when viewed from above; 6) Corbicula, penicillum and rastellum lost.

The shape of the head, with its small eyes and clypeus (characters 1 to 3), is unusual among the stingless bees. It is possible that this feature of the head is correlated somewhow with the thieving way of life, since they obtain their food exclusively by robbing colonies of other stingless bees. The lack of corbicula, penicillum, and rastellum are obviously correlated with this way of life.

Characters 4 and 5 are not unusual among stingless bees. A short scutellum for instance, is also found in *Hypotrigona,* and a bituberculate labrum is found in certain species of the subgenus *Trigona* (such as *T. pallida* and *T. chanchamayöensis*).

Although *Cleptotrigona* and *Lestrimelitta* appear superficially similar, mainly in relation to their heads, they are quite different in the following characters:

	Cleptotrigona	*Lestrimelitta*
1.	Eyes more than twice as long as broad, inner margins slightly converging ventrally	Eyes less than twice as long as broad, inner margins subparallel
2.	Third antennal segment subequal to fourth	Third antennal segment longer than fourth
3.	Distance from apicolateral extremity of clypeus to margin of eye subequal to width of flagellum	Distance from apicolateral extremity of clypeus to margin of eye less than width of flagellum
4.	Length of malar space greater than width of flagellum	Length of malar space subequal to width of flagellum
5.	Anterior border of labrum broadly rounded, outer surface slightly concave	Anterior border of labrum pointed, outer surface conspicuously concave
6.	Intertentorial passage pear-shaped, Fig. 25	Intertentorial passage rectangular, Fig. 26
7.	Prothoracic endosternum with supraneural bridge complete, Fig. 27	Prothoracic endosternum with supraneural bridge incomplete, not fused along midline, Fig. 28
8.	Forewing venation very weak	Forewing venation very strong
9.	Hind wing with six hamuli	Hind wing usually with five hamuli (six in Costa Rican forms)
10.	Gonostylus flat and wide, its length equal to width of flagellum, Fig. 7	Gonostylus more or less cylindrical and small, its length about half the width of flagellum
11.	General size smaller, about 4 mm in length or less	General size larger, about 6 mm in length
12.	Brood cells arranged in clusters	Brood cells arranged in horizontal combs

There is a larger number of characters in which they differ from the number they have in common. This supports the idea that *Cleptotrigona* and *Lestrimelitta* are not as closely related as they were thought to be. According to Table 3, *Lestrimelitta* is much more specialized than *Cleptotrigona* and very likely represents a later development. *Cleptotrigona* retains such primitive features as a flat gonostylus, a cluster type nest, and relatively small size. If we accept that the similarities between *Cleptotrigona* and *Lestrimelitta* are parallelisms, then the problem of their geographical distribution is self explanatory. Otherwise, as Portugal-Araújo (1958) has indicated, "This genus is considered by several workers as being quite specialized, suggesting a recent origin. If this were the case, the geographical distribution ought to be restricted, occupying only one continent. However, *L. cubiceps* is found in Africa and the other species in tropical America". This dilema led him to reach the following conclusion: "The genus *Lestrimelitta,* to judge by its geographical distribution in America and Africa, looks to be an old group."

There is one final point which should be clarified. In all the *Cleptotrigona* examined, the forewing had six hamuli, while most of the South American *Lestrimelitta* had five. These five hamuli are arranged in two groups: the basal, composed of three and the other group of two, with a small gap in between, suggesting that there were formerly six hamuli. In Costa Rica, however, all the specimens observed had one additional hamulus, which is thicker and different from the others, and is located basally in the first group, the gap remaining between the two groups (now composed of four and two). This suggests that formerly, *Lestrimelitta,* at least *L. limão,* had seven hamuli instead of six or five. Few specimens from South America were observed with six, like those of Costa Rica. Schwarz (1948) reported specimens with four or seven, but apparently these are very rare.

Paralellisms between *Melipona* and *Meliponula* have already been discussed in a previous work (Wille, 1963). At that time, however, *Meliponula* was regarded as a major phylogenetic stock, intermediate between *Trigona* and *Melipona.* The *Melipona*-like characters of *Meliponula* are the following:

1. Very robust (about 8 mm in length), with a short and stout abdomen that gives it an unmistakable appearance of *Melipona.*
2. Pubescence very dense on the upper half of the head and the thorax.
3. Integument tessellate, with the head, thorax and legs minutely granulose, and the abdomen finely dull-reticulate.
4. The combination of this type of integument and pubescence results in the propodeum of *Meliponula* being tesselate and pubescent, like all the species of *Melipona.*
5. The thoracic portion of the dorsal vessel is arched between the dorsal longitudinal muscles of the thorax.

Although in the previous work *Meliponula* was regarded as intermediate between *Trigona* and *Melipona,* it was placed closer to *Trigona.* It is now obvious, however, that *Meliponula* does not occupy an intermediate position between *Trigona* and *Melipona.* Its similarities with *Melipona* are paralellisms. Actually it is closer to *Meliplebeia* than to any other group of stingless bees; this is indicated by the flat gonostylus, a better developed sting structure, the nature of the inner surface of hind tibia, lack of rastellum, etc. For further information see Wille, 1963.

As mentioned before there are also some paralellisms between *Partamona* and *Axestotrigona,* and between *Plebeia* and *Meliplebeia. Partamona* and *Axestotrigona* are superficially similar; they have the hind tibia spoon-shaped (*Lepidotrigona* also has a similar corbicula, but it is quite different in other respects), and the inner side of the hind tibia lacks any depressed area along the posterior rim. These similarities are mere paralellisms, since *Axestotrigona* belongs to the African complex, those having a flat gonostylus and a more developed sting. Furthermore, *Axestotrigona* lacks a rastellum, another African feature (found in *Meliplebeia, Meliponula, Hypotrigona,* restricted to a much smaller area in *Dactylurina,* and perhaps lost in *Cleptotrigona* due to its mode of life). *Axestotrigona* also has the tegument very densely tesselate and dull and the abdomen very robust, reinforcing its relationship

TABLE 3

Levels of specialization

Groups of Meliponinae	Relative level of specialization (see text)
Axestotrigona	1
Meliplebeia	1
Hypotrigona	4
Plebeia	4
Nogueirapis	4
Trigonisca	5
Cleptotrigona	6
Scaura	7
Oxytrigona	7
Lepidotrigona	7
Cephalotrigona	7
Paratrigona	7
Partamona	8
Scaptotrigona	8
Tetragona	8
Meliponula	8
Lestrimelitta	10
Trigona	11
Nannotrigona	13
Dactylurina	13
Melipona	22

with *Meliponula* and most *Meliplebeia* (or the African complex). *Axestotrigona,* however, may represent an old survival group from the ancestral stock containing all the stingless bees without any depressed area on the inner surface of the hind tibia.

CLASSIFICATION OF MELIPONINAE

Evolutionary levels: Some of the earliest Meliponinae were very likely minute *Plebeia*-like bees, all of which should have been already undergoing reduction of the sting apparatus and the veins of the fore wing, and no doubt all had the primitive characters listed in Table 2. There are two groups which can be regarded as the most primitive (*Axestotrigona* and *Meliplebeia*), three primitive (*Hypotrigona, Plebeia* and *Nogueirapis*), four specialized (*Lestrimelitta, Trigona, Nannotrigona* and *Dactylurina*), and one very specialized *(Melipona).* The others can be considered as intermediate. In order to evaluate the evolutionary levels of specialization among the different groups of Meliponinae, relative values of characters were given in Table 2. With these data one can derive Table 3, indicating the levels of specialization among the different groups.

TABLE 4

Numbers of genera and subgenera used by various authors in the classification of stringless bees

Author	Genera	Subgenera
Illiger (1806)	1	0
Jurine (1807)	1	0
Latreille (1809)	2	0
Lamarck (1817)	1	0
Lepeletier (1825)	3	0
Lepeletier (1836)	1	3
Smith (1863)	2	0
Ducke (1902)	1	2
Friese (1903)	2	2
Cockerell (up to 1934)	2	7
Schwarz (up to 1948)	3	18
Moure (1951)	16	20
Moure (up to 1961)	32	26
Present paper	8	15

The most specialized of all the genera of Meliponinae is *Melipona* (Table 1). The difference between *Melipona* and the other stingless bees is so significant that *Melipona* is segregated as the tribe Meliponini, as suggested in the first part of this paper.

The genus *Trigona,* a large and heterogeneous group, includes the remaining stingless bees. None of its species has either a flat gonostylus (except the African *Plebeia*) nor the second sting valvulae fused into a short stylet and the first valvulae forming short lancets. Also, none of its species shows unique features like those found in *Cleptotrigona, Lestrimelitta, Dactylurina, Meliponula,* and *Melipona.* This genus is the only one which deserves to be subdivided into several subgenera (see phylogenetic tree).

The subgenera of *Trigona:* This section is intended primarily to defend the recognition of certain groups as subgenera, and the relegation of some names to synonymy.

1. *Tetragona:* Included here in the subgenus *Tetragona* are not only *Tetragona s. str.*, but also groups that have been named *Geotrigona, Duckeola, Tetragonisca, Ptilotrigona, Frieseomelitta, Homotrigona, Heterotrigona, Platytrigona, Lophotrigona, Tetragonula, Tetragonilla, Geniotrigona, Odontotrigona,* and *Tetrigona.*

Moure (1961) recognizes six genera of American *Tetragona (Tetragona, Geotrigona, Duckeola, Tetragonisca, Ptilotrigona,* and *Frieseomelitta*). The genus *Tetragonisca* was erected by Moure in 1946 to include *Trigona jaty, T. pfeifferi* and later *T. buckwaldi,* but in 1951 he regarded *Tetragonisca* as a subgenus of his restricted genus *Trigona.* In his opinion those three species are more closely related to *Trigona s. str.*, than they are to *Tetragona,* because they all have on the inner surface of the hind basitarsus a bristleless, sericeous area of suboval shape just below the neck, a character which is also shared by all *Trigona s. str.* However, *Tetragonisca* more nearly resembles *Tetragona* in the characteristics of the labrum, mandible, and epistomal suture; the only important character in common with *Trigona s. str.* is the sericeous area just mentioned. Furthermore, the same character is found in the Indo-Malayan *Tetragona,* suggesting that the sericeous area on the basitarsus is an indication of the general relationship between *Tetragonisca* and *Trigona*, and not of the more specific relationship between *Tetragonisca* and *Trigona s. str.* The close relationship between *Tetragonisca* and the Indo-Malayan *Tetragona* is well indicated by *T. pfeifferi,* which like most Indo-Malayan species of *Tetragona* has a distinctive pollen press * (Fig. 29). *Duckeola* (Moure, 1944), *Geotrigona* (Moure, 1943) and *Ptilotrigona* (Moure, 1951) are all regarded by Moure at the present time as subgenera of the genus *Trigona* as understood by Moure (1961). That they represent secondary phyletic lines is indicated by the characters by which they are differentiated. These characters are limited in number and rather wide-spread among other stingless bees. *Geotrigona* is characterized by the lack of yellow markings, vertex produced into a weak crest, and a relatively short, wide and subtriangular abdomen, with the dorsal surface slightly convex. However, the same type of abdomen and a crest are also found in many Indo-Malayan *Tetragona. Duckeola* consists of only one species (*T. lurida*), which has been separated by its triangular hind tibia, large number of hamuli (8), and by its strongly crested vertex, but the same characters are found in some Indo-Malayan

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* In the stingless bees the pollen press is represented by a rather weakly arched carina which is fringed with relatively small hairs.

Tetragona. Ptilotrigona, also consisting of one species (*T. heideri*), has been set apart mainly because the basal area of its propodeum is covered with hairs and punctures. However, as was the case with the other groups just discussed, this character is shared also by some Indo-Malayan species of *Tetragona. Frieseomelitta* has been accepted as a subgenus by Moure (1961, 1963) and other South American workers, mainly to place together the six American *Tetragona* which make a cluster type of brood arrangement. Three of them have been found to have a very primitive type of communication in relation to food sources (Kerr, 1969). This type of communication is, however, not a great deal different from that found in *Trigona jaty;* furthermore, one of the *Frieseomelitta* species, *T. varia,* has apparently a communication system similar to that of *Partamona. T. varia* is known to have a chromosome number of 15 (*T. braunsi,* a *Hypotrigona,* has n=13 to 15). Moure (1963) listed the morphological characters of *Frieseomelitta* as follows: a very narrow yellow stripe around the eyes, and a higher number of hamuli. *Frieseomelitta,* like the others discussed above, probably represents a secondary phyletic line; the nature of its characters, in my opinion, is not reliable enough to justify its separation from *Tetragona.*

Heterotrigona was erected by Schwarz (1939) as a subgenus of *Trigona* to include two species of Indo-Malayan stingless bees (*itama* and *erythrogastra*). According to Schwarz, *Heterotrigona* is "closely related to the subgenera *Trigona* and *Tetragona* and especially to the latter". The subgenus was erected mainly because the male of *Heterotrigona* has a pear-shaped hind tibia, with its apical margin prolonged into a blunt, crescentic spine. However, it should be pointed out that males possessing such specialized modifications are not uncommon among the bees, striking examples being found among *Calliopsis,* eucerine bees, euglossine bees, etc. The females associated with such modified males often do not show any departure from their respective genera. Another character by which *Heterotrigona* has been set apart is the possession of only one tooth on each mandible. Although no other *Tetragona* has unidentate mandibles, the presence of one or two teeth does not seem to be very significant. Among the species of the subgenus *Trigonisca,* both types are found. Moreover, the distinction between unidentate and bidentate mandibles is not always clear, as is shown in some species of *Melipona.* That *Heterotrigona* should be included in *Tetragona* is indicated not only by all the characters in common, but also by the presence of a distinctive pollen press, already mentioned, which is found in most Indo-Malayan and one American species of *Tetragona,* and also by having the bristleless sericeous area on the hind basitarsus, a character common to most Indo-Malayan and three American *Tetragona.*

Besides *Heterotrigona,* Moure (1961) divided the Indo-Malayan *Tetragona* into eight genera (*Homotrigona, Platytrigona, Lophotrigona, Tetragonula, Tetragonilla, Geniotrigona, Odontotrigona* and *Tetrigona*). Unfortunately, those groups, as was the case with *Tetragonisca,* were made typologically by selecting certain characters, such as a sericeous area on the basitarsus, the posterior distal angle of the hind tibia, projected scutellum, long flagellum, or large malar area, etc., and then defining the genera by them, rather than by considering the entire constellation of characters presented. Any form lacking a particular feature is placed in a new genus. I was unable to find any consistent differences between the American and Indo-Malayan *Tetragona.* The apparently most distinctive characters of certain species of the Indo-Malayan *Tetragona,* namely the peculiar pollen press, the sericeous area on the basitarsus, and the projected scutellum, are also found in *T. pfeifferi,* an American *Tetragona.*

TABLE 5

Characters differentiating the groups usually united under the name Hypotrigona

Indo-Malayan and African species (*Hypotrigona* proper)	American species (*Trigonisca*)
Distance from apicolateral extremity of clypeus to margin of eye less than width of flagellum	Distance from apicolateral extremity of clypeus to margin of eye subequal to or greater than flagellar width
Length of malar space much less than width of flagellum	Length of malar space greater than width of flagellum, except in *T. longitarsus* in which it is subequal
Hairs of labial palpi and maxilla with their tips bent or hooked	Hairs of labial palpi and maxilla with their tips straight
Contour of intertentorial passage pear-shaped, Fig. 25	Contour of intertentorial passage usually rounded, Fig. 24
Median angle of ventral border of second phragma forming a right angle	Median angle of ventral border of second phragma usually obtuse
Hind tibia more or less claviform with posterior distal extremity rounded	Hind tibia triangular with posterior distal extremity produced into an angle
Pterostigma smaller, its length usually 3.4 times its width	Pterostigma larger, its length usually 3.2 times its width
Marginal vein (Rs) slightly arched basally	Marginal vein (Rs) strongly arched basally, Fig. 23
Petiole at base of first median cell shorter than cu-v	Petiole at base of first median cell as long as cu-v
Second valvulae not meeting at an angle	Second valvulae meeting at right angle

2. *Hypotrigona* and *Trigonisca.* The American species usually placed in *Hypotrigona* are separated in the present work as a different subgenus from the *Hypotrigona* of Africa and Asia. Moure (1961) divided the Indo-Malayan *Hypotrigona* into the genera *Pariotrigona* and *Lisotrigona,* and the African ones into *Liotrigona* and *Hypotrigona. Trigonisca* and *Hypotrigona,* as recognized in this paper, are similar in many ways, summarized as follows: very small bees, ranging from 2 to 4 mm in length; antennal sockets usually well below middle of eyes, so that length of supra-antennal area is slightly more than twice the length of infra-antennal area; scutellum viewed from above usually not covering mesal portion of metanotum; median elevation of inner surface of hind tibia usually covered with dense hairs throughout its length, leaving a bare, relatively narrow, posterior flange, about one-fifth width of tibia; pterostigma large, its length less than four times its width. Careful examination, however, shows great differences between the American and the Afro-Indian groups*, as is indicated in Table 5.

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* The same opinion was expressed by Moure in a letter to me.

Because of these characters the American Hypotrigonas are called here *Trigonisca,* which is one of the four names (*Trigonisca, Leurotrigona, Celetrigona,* and *Dolichotrigona*) used by Moure (1950) as American subgenera of the genus *Hypotrigona* as he understands it. The few Indo-Malayan species of *Hypotrigona* conform well with the African species.

3. *Plebeia:* The subgenus *Plebeia,* as here understood, includes groups called by Moure *Plebeia s. str., Friesella, Mourella, Schwarziana, Plebeina,* and *Austroplebeia. Mourella* was erected by Schwarz (1948) as a subgenus of *Trigona* to include *T. caerulea.* It was separated from *Plebeia* mainly because of its dark metallic blue color and hairy basal area of the propodeum. Although those two characters are unique among the species of *Plebeia,* in my opinion they are not sufficiently marked to be expressed taxonomically. The same can be said of *Friesella,* which was first erected by Moure (1946) as a genus to include *T. schrottkyi.* Later (Moure, 1951) he regarded it as a subgenus of the genus *Plebeia.*

Schwarziana, which was proposed by Moure (1943) to include a rather isolated species (*T. quadripunctata*), can no longer be considered as distinct from *Plebeia,* due to the discovery of a species (Wille, 1960) described as *T. (Plebeia) intermedia. Schwarziana* was set apart mainly by its large size (7 mm), the finely granulose and dull cuticular surface of its head and thorax, the small scutellum which does not cover or only partially covers the mesal portion of the metanotum, and the large number of hamuli (8). *T. intermedia* is about 6 mm in length, its cuticular surface is between that of *Plebeia* proper and *Schwarziana,* its scutellum resembles that of *Schwarziana,* and it has 7 hamuli.

Plebeina and *Austroplebeia* were erected by Moure (1961) as genera to include the African and Australian *Plebeia.* However, no differences were reported between them and the American *Plebeia. Plebeina,* however, has a flat gonostylus, which suggests that it belongs to the complex of African stingless bees, as already indicated. Since *Plebeia* and *Plebeina* are at about the same level of specialization they appear very closely related, and from the pure taxonomic point of view *Plebeina* should not be regarded as a group.

4. *Scaura:* In 1946 Moure erected the genus *Schwarzula* to include *T. timida* but later (Moure, 1951) he regarded *Schwarzula* as a subgenus of the genus *Scaura.* Although the species *timida* is distinctly a *Scaura,* as indicated by its large basitarsus, it is peculiar in having clearly bidentate mandibles (mandibles of other *Scaura* lack teeth or are very weakly bidentate), wider malar space, and the posterior rim of the inner surface of the hind tibia extremely narrow. I do not think that these few differences justify nomenclatural recognition of *Schwarzula.*

5. *Paratrigona:* Two species of *Paratrigona (impunctata* and *isopterophila)* were placed by Moure (1951) in the subgenus *Aparatrigona* because the males posses a somewhat modified fifth sternum. However, the same arguments given in the case of *Heterotrigona* are also appropiate here, namely that the formation of new subgenera based entirely on one structural modification of the males is not justifiable.

6. *Nannotrigona* and *Scaptotrigona:* Although these subgenera are related to each other, they are sufficiently distinct to be separated, as indicated in Table 6. *Nannotrigona* is a much more specialized group (Table 3) than *Scaptotrigona.*

TABLE 6

Differentiation of Scaptotrigona *and* Nannotrigona

Scaptotrigona	*Nannotrigona*
Cuticular surface of head and thorax finely punctate	Cuticular surface of head and thorax very coarsely pitted
Mesepisternum evenly bent anteriorly	Mesepisternum sharply bent anteriorly so that an anterior surface is separated from a lateral one
Scutellum, as seen from above, extended backward slightly, not as far as end of propodeum, covering at most, mesal portion of metanotum and part of propodeum	Scutellum, as seen from above, extended backward as far as end of propodeum, thus covering mesal portion of metanotum and propodeum
Posterior border of scutellum rounded	Posterior border of scutellum emarginate
Length of malar space greater than width of flagellum, except in *T. tubiba* in which it is subequal	Length of malar space much less than width of flagellum
Distance from apicolateral extremity of clypeus to margin of eye greater than width of flagellum, except in *T. tubiba* in which it is subequal	Distance from apicolateral extremity of clypeus to margin of eye less than width of flagellum
Hairs of labial palpi and maxilla with straight tips	Hairs of labial palpi and maxilla with hooked tips
Width of horizontal plate of mesosternal apophysis greater than twice width of flagellum	Width of horizontal plate of mesosternal apophysis less than twice width of flagellum
Corbicula occupying slightly more than half of tibia	Corbicula occupying one-third to almost half of tibia
Hamuli 6 to 7	Hamuli 5

7. *Partamona: Trigona zonata* was placed by Schwarz (1948) in a new subgenus, which he called *Parapartamona,* mainly because of its cuticular surface, which is very finely granulose and dull, and its long propodeum. However, the differences between *T. zonata* and other species of *Partamona* are in my opinion not significant enough to justify subgeneric recognition. Indeed *T. zonata* presents a series of characters which are typical of *Partamona* proper, for example, the upper halves of the lateral portion of the epistomal suture are subparallel while below, the lateral portions of the suture become strongly divergent (Fig. 22). This character is found elsewhere only in the subgenus *Trigona.* Also the hind tibia is spoon-shaped, the corbicula occupying practically its whole surface. Furthermore, *T. zonata* and other *Partamona,* alone among the species of *Trigona* without a rim or flange on the inner surface of the hind tibia, have the basal area of the propodeum punctate and hairy.

8. *Nogueirapis:* This subgenus was erected by Moure in 1953 to include the species described by Friese as *Trigona butteli,* a rare form from South America. More recently however, *T. silacea,* the fossil stingless bee from the amber of Chiapas, Mexico, has been included in *Nogueirapis,* as well as the living *T. mirandula* ranging from Costa Rica to Colombia (Wille, 1959). Although *Nogueirapis* is related to *Partamona,* it presents a series of characters, such as coloration, size, width of the clypeus, type of epistomal suture, location of antennal sockets, basal area of propodeum, shape of hind tibia, submarginal angle, etc., which are different from *Partamona.* Therefore, *Nogueirapis* is considered here a valid subgenus.

The subgenera *Lepidotrigona, Cephalotrigona* and *Oxytrigona* were originally described in this status and have not been subdivided or transferred to other groups. For this reason they are not commented upon.

After writing this work, Dr. C.D. Michener brought to my attention a very recent paper by Moure and Camargo (1978) in which they proposed that *Trigona dominicana,* which I described with Chandler as a *Hypotrigona,* pertains to the genus *Plebeia.* They based their decision entirely on our description, mostly in reference to the yellow maculation and some minor details of the wing venation. I still insist that *T. dominicana* is a *Hypotrigona* and not a *Plebeia.* First, the inner side of the hind tibia has a narrow bare posterior depressed rim, but much wider than in *Plebeia.* In the original description this proportion is mentioned as (3:9) = 0.099:0.297 mm, which fits in my Table 2 in 12b. Second *T. dominicana* has a very weak rastellum and a vestigial penicillum, typical of *Hypotrigona* (Table 12, No.6 and 7) and not of *Plebeia.* Finally Moure and Camargo mentioned in page 564 the following: "The existence of fossil *Plebeia* in Dominicana was confirmed by the superficial study of another species in amber from the same geological formation. It is much darker and of different size". It happens that a friend of mine, Dr. Ronald Echandi, brought me a piece of amber with three bees from Dominicana, and those bees are apparently the same that Moure and Camargo studied superficially. These bees are actually *Plebeia*, they are black, without yellow markings, with well-developed rastellum and penicillum, and the inner side of the hind tibia has a typical *Plebeia* rim (1:9), which fits in my Table 2 in 12a. At the end of their paper they propose a new genus *(Kelnermelia)* to include *Trigona (Hypotrigona) eocenica,* described by Kelner-Pillault (1970). I consider this a mere guess since the specimen could be a male, and the inner surface of the hind tibia is not visible.

ACKNOWLEDGMENTS

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RESUMEN

El presente estudio trata de indicar las posibles tendencias evolutivas y las interacciones de los varios grupos de las abejas Melipónidas del mundo. También se propone una nueva clasificación para la subfamilia Meliponinae.

El trabajo demuestra que estas abejas tuvieron su centro de origen en Africa, basado en lo siguiente: 1) En Africa se encuentran las Melipónidas más primitivas, las cuales tienen un aguijón mejor desarrollado que los demás grupos, 2) La presencia de un fósil en ambar del Báltico del Eoceno superior, 3) La aceptación general de la deriva de los continentes. El encuentro en Europa de un Melipónido fósil del Eoceno superior, hace difícil aceptar que estas abejas tuvieran su origen en América del Sur. Como es sabido, este continente se encontraba completamente aislado después de su separación con Africa durante el Cretáceo medio. El puente de unión entre Norte América y Sur América se estableció en el Plioceno. La extrema aridez del Plioceno Africano podría explicar el Porqué hoy día existen relativamente pocas especies en Africa. Como prueba de ésto se hace una comparación de lo que pasó con la evolución del guapinol (*Hymenaea*), que también se originó en Africa. Hoy día se conocen 16 especies de este género en América, y sólo una en Africa.

El estudio sugiere también varios paralelismos entre los géneros de las abejas Africanas con algunos grupos de los otros continentes. Por ejemplo entre *Cleptotrigona* y *Lestrimelitta,* entre *Dactylurina* y *Tetragona,* entre *Meliplebeia* y *Plebeia* y entre *Meliponula* y *Melipona.*

La nueva clasificación que se presenta aquí trata de demostrar y defender el reconocimiento de ciertos grupos como géneros y subgéneros, al mismo tiempo que relega otros nombres a la sinonimia. En este trabajo se reconocen 8 géneros y 15 subgéneros en el género *Trigona.*

Fig. 1. Ventral nerve cord of *Trigona fulviventris*

Fig. 2. Ventral nerve cord of *Melipona marginata*

Fig. 3. Ventral nerve cord of *Melipona nigra (= flavipennis)*

Fig. 4. Dorsal vessel of *Trigona* sp.

Fig. 5. Dorsal vessel of *Melipona marginata*

Fig. 6. Sting apparatus of *Meliponula bocandei*

Fig. 7. Sting apparatus of *Cleptotrigona* and African *Plebeia*

Fig. 8. Sting apparatus of most stingless bees.

Fig. 9. Posterior view of head of *Cleptotrigona* and *Lestrimelitta*

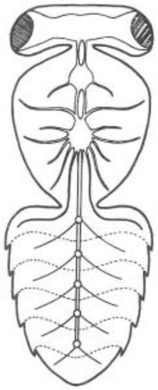
Fig. 10. Posterior view of head of most stingless bees.

Fig. 11. Mandible of *Trigona* (*Cephalotrigona*) *capitata*

Fig. 12. Mandible of most stingless bees.

Fig. 13. Mandible of *Trigona (Paratrigona)* sp.

Fig. 14. Mandible of *Trigona (Trigona)* sp.



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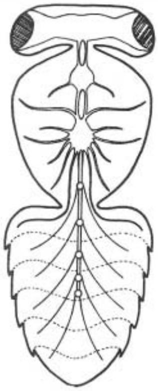

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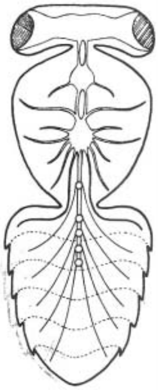

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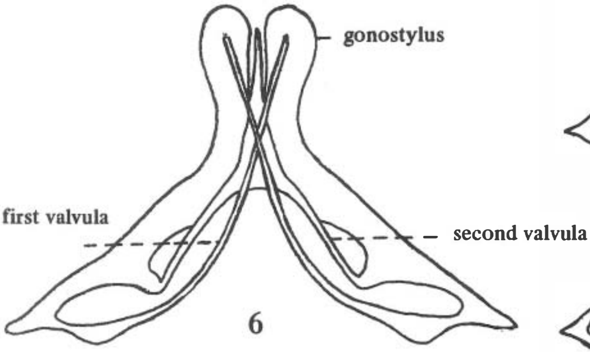

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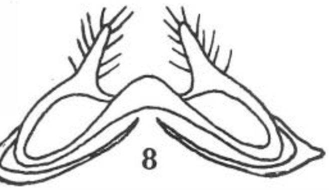

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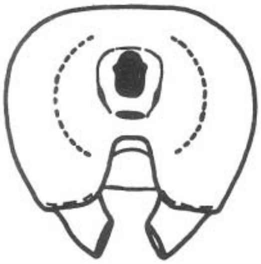

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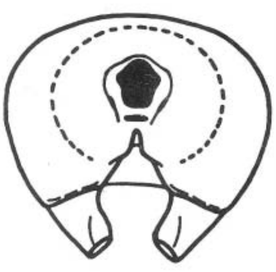

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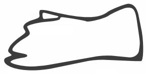

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Fig. 15. Inner view of hind tibia of *Trigona (Plebeia)* sp.

Fig. 16. Inner view of hind tibia of *Trigona (Trigonisca) longitarsus*

Fig. 17. Inner view of hind tibia of *Trigona (Tetragona)* sp.

Fig. 18. Hind tibia of *Trigona (Lepidotrigona) nitidiventris*

Fig. 19. Hind tibia of *Trigona (Scaura)* sp.

Fig. 20. Outer view of hind tibia of *Meliponula bocandei*

Fig. 21. Head of *Trigona (Tetragona)* sp.

Fig. 22. Head of *Trigona (Trigona)* sp.

Fig. 23. Fore wing of *Trigona (Trigonisca)* sp.

Fig. 24. Dorsal view ot tentorium of *Trigona (Trigonisca)* sp.

Fig. 25. Dorsal view of tentorium of *Cleptotrigona* and *Trigona (Hypotrigona)* sp.

Fig. 26. Dorsal view of tentorium of *Lestrimelitta.*

Fig. 27. Dorsal view of prothoracic endosternum of *Cleptotrigona*

Fig. 28. Dorsal view of prothoracic endosternum of *Trigona (Tetragona) nigra*

Fig. 29. Outer view of basitarsus of *Trigona (Tetragona) atripes* showing pollen press and additional row of hairs.

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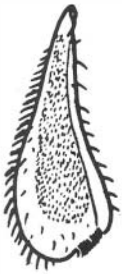

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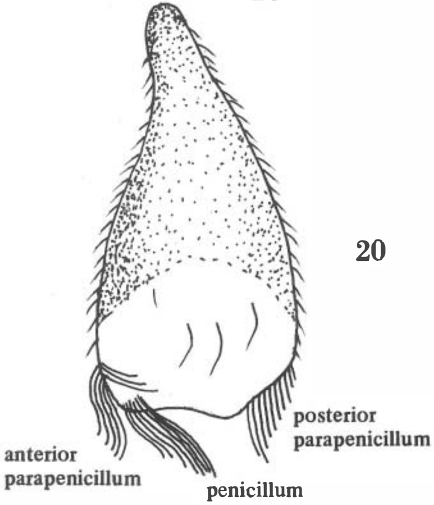

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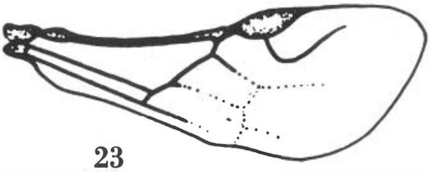

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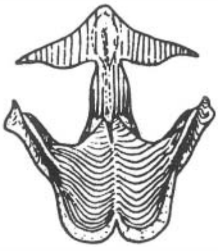

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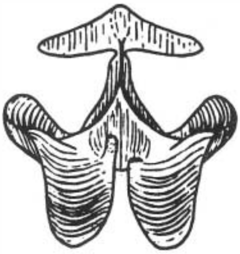

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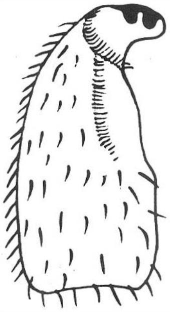

29

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Fig. 30. Phylogenetic tree of the stingless bees. The following are explanatory comments:

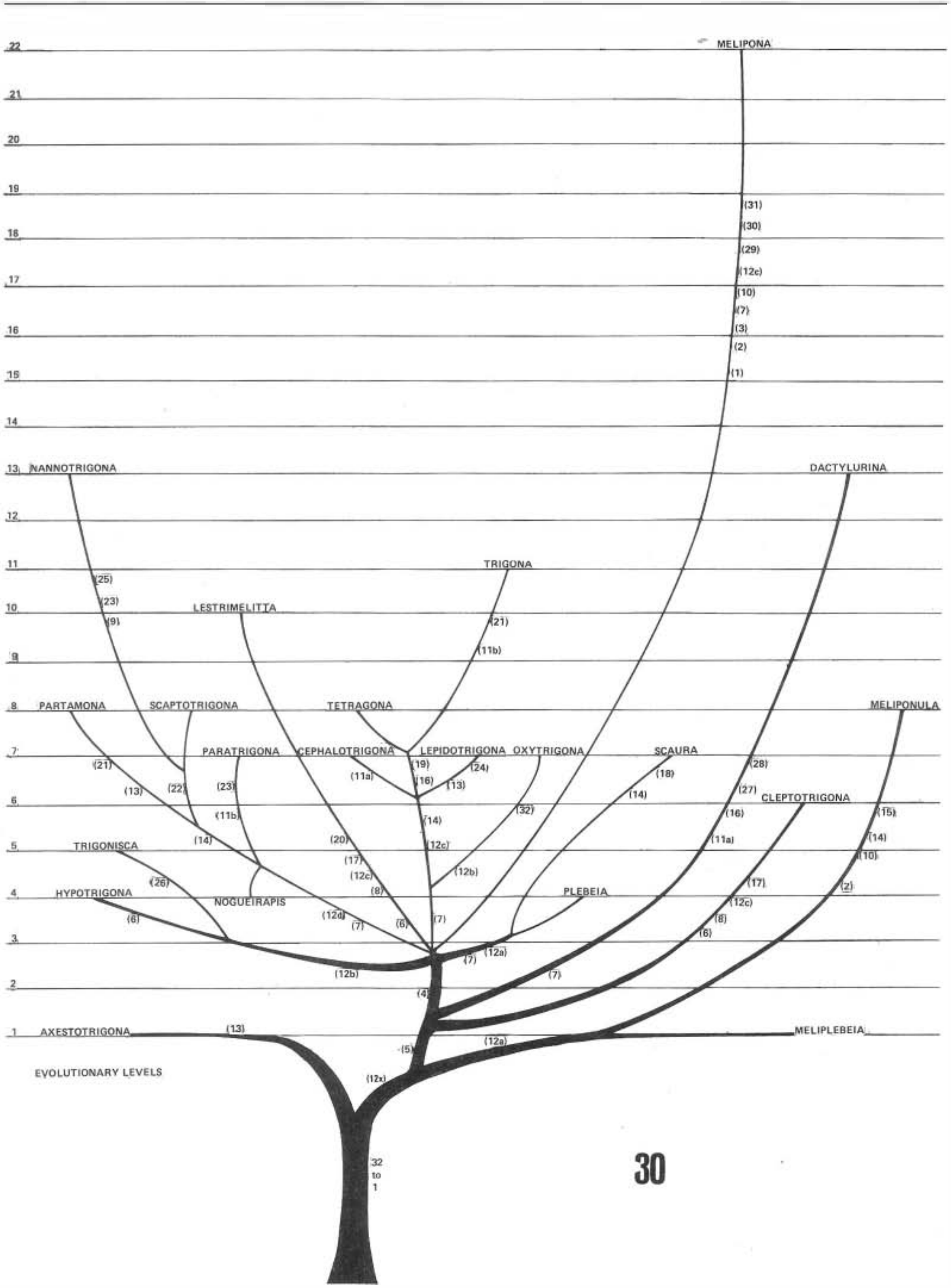
a. Numbers in parentheses indicate derived characters. The characters are described and numbered in Table 2.

b. The thickest lines of the tree mean African origin (the *Plebeia* line starts thick because of the African *Plebeia*)

c. (12X) indicates any of the derived alternatives of 12, such as (12a) (12b) and (12d), as shown in Table 2.

d. (14) The primitive character is retained in few *Tetragona,* like *T. leucogastra*

e. (23) The primitive character is retained in some species of *Paratrigona*


22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
MELIPONA
(31)
(30)
(29)
(12c)
(10)
(7)
(3)
(2)
(1)
NANNOTRIGONA
DACTYLURINA
TRIGONA
(25)
(23)
(9)
LESTRIMELITTA
(21)
(11b)
PARTAMONA
SCAPTOTRIGONA
TETRAGONA
MELIPONULA
PARATRIGONA
CEPHALOTRIGONA
LEPIDOTRIGONA
OXYTRIGONA
SCAURA
(21)
(13)
(22)
(23)
(11b)
(14)
(11a)
(19)
(16)
(24)
(13)
(14)
(18)
(28)
(27)
CLEPTOTRIGONA
(16)
(32)
(15)
TRIGONISCA
(20)
(12c)
(11a)
(14)
(10)
(26)
(17)
(12c)
(8)
(12b)
(17)
(12c)
(2)
HYPOTRIGONA
NOGUEIRAPIS
PLEBEIA
(6)
(12d)
(7)
(6)
(7)
(8)
(6)
(7)
(12a)
(12b)
(7)
(4)
AXESTOTRIGONA
(13)
MELIPLEBEIA
(5)
(12a)
(12x)
EVOLUTIONARY LEVELS
32
to
1

30

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