Review article

# Systematics, phylogeny and biogeography of the Meliponinae (Hymenoptera, Apidae): a mini-review

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**Summary** — The main proposals for systematics, phylogeny and biogeography of the Meliponinae, and the polarity and significance of some morphological characters are discussed. Although a set of probable synapomorphies is suggestive of the Meliponinae as a co-phyletic group with the Apinae, Bombinae and Euglossinae, the relationships with these subfamilies remain unclear. The distributional pattern and fossil record are indicative of greater antiquity for the Meliponinae and suggestive of an independent origin or an early divergence from a proto-other Apidae branch. The sister-group relationship between Malayan and neotropical Meliponinae (*Tetragona-Tetragonisca* line and possibly *Trigonisca–Pariotrigona, Lisotrigona*), and the probable relationship between *Austroplebeia* and the neotropical *Plebeia line*, are suggestive of a West-Gondwanan origin for the Meliponinae, with 2 main dispersal routes *via* the holarctic and panaustral regions.

systematics / biogeography / Apidae / Meliponinae / phylogeny

## ON THE RELATIONSHIPS OF THE MELIPONINAE AND OTHER APIDAE

Sakagami and Michener (1987) and Michener (1990) presented strong arguments in favor of the hypothesis that the Meliponinae (M), Apinae (A), Bombinae (B) and Euglossinae (E) constitute a holophyletic clade, the probable sister-group of the Xylocopinae. They included certain characters – absence of basitibial and pygidial plates and nests usually constructed in large or irregular cavities, cells built up

rather than excavated in the substrate – as possible synapomorphies, in addition to the well known corbicula and rastellum (present in females, except in parasitic and cleptobiotic forms and in queens of the highly eusocial groups). Michener (1990) also included other possible synapomorphies (hind basitarsus of female articulated near anterior end of apex of tibia, reduced maxillary palpus, 1- or 2- segmented), and other characters, such as form and type of cephalic and thoracic salivary glands and hypopharyngeal glands

(see also Cruz-Landim, 1967), and commented that this association of character states is an indication "that the 4 subfamilies of Apidae are related to one another, ie, that no one of them is an anthophorid group that has convergently evolved the external features of Apidae". Despite these deductions, Michener (1990) did not exclude the possibility that the main characteristic of the Apidae, the complex pollen-manipulating behavior and associated structures, could have arisen independently in 2 or more of the groups included in the Apidae, considering the distinctive mechanical and morphological solutions they present (rastellum and auricula in A and B, rastellum or posterior parapenicillum and penicillum in M, and an auricula-like structure in E; cf Michener et al, 1978; Wille, 1979a). Even the corbicula (a bare or sparsely haired area on the outer surface on the hind tibia, used for the transport of both sticky material for nest construction and pollen), the principal synapomorphy, and one that, in the opinion of Michener et al (1978), precedes the origin of the highly derived pollen-manipulating behavior and associated structures, is not an exclusive attribute of the Apidae. A corbicular structure also occurs in Canephorula apiformis, an Anthophorinae from Argentina (cf Friese, 1920; Michener et al, 1955). Some of the other possible synapomorphies suggested by Sakagami and Michener (1987) and Michener (1990), ie absence of basitibial and pygidial plates and reduced maxillary palpus indicate loss and may occur independently as in some other Apoidea. Although the set of characters considered here is more indicative of holophyly for the Apidae, the situation becomes more complex when one searches for the synapomorphies indicative of relationships among the 4 taxa, as verified by the different proposals of phylogeny. Winston and Michener (1977) and Kimsey (1984) suggested M as the sister-group of the other Apidae;

Winston (1979), in a study of the mouthparts, suggested a relationship between M and the Xylocopinae, or an early divergence of M from the other Apidae. Plant and Paulus (1987) considered E as the oldest branch, a sister-group of the other Apidae. Michener (1990) presented 5 of the 15 possibilities of relationship among the 4 taxa; he considered the cladograms where M–A appears as a sister-group of B–E, and E as a sister-group of B, A–M more probable; however, from the biogeograhic point of view and possible greater antiquity of M, he also considered reasonable the cladograms where this taxa appears as a sister-group of E, B and A. Prentice (1991) suggested E and B as older branches and A–M as sister-groups (as originally proposed by Michener, 1944).

In recent papers, based on mitochondrial and ribosomal DNA sequences, Cameron (1991) and Sheppard and McPheron (1991) proposed the Meliponinae and Bombinae as sister-groups. Although this refined methodological approach may constitute a valuable tool for taxonomy and systematics, the number of Apidae and non-Apidae bees presently analysed is too small to allow inference of phylogenetic relationships.

As previously pointed out by Camargo (1989), none of the propositions on phylogenetic relationships of the Meliponinae with the other Apidae considered congruity with the biogeographic patterns, apart from some considerations presented by Michener (1990:82). M is widely distributed, ranging through the pantropical and southern subtropical regions (cf Moure, 1961); the neotropical region, Africa, south of the Sahara, Madagascar, the Malayan region, s lat including the islands on the east of the Wallace's line (New Guinea, Sakagami et al, 1990), the eastern Indian subcontinent, New Guinea, and northeastern Australia, with several hundred species and many supra-specific taxa (21 recent genera, according to Michener 1990; and 54 accord-

ing to Camargo 1989, besides 3 extinct genera). This distribution pattern and the antiquity (the oldest known bee fossil, *Trigona prisca* from late Cretaceous New Jersey – USA amber, 96–74 mya, is very similar to the recent species of *Trigona s str* from the neotropics; *cf* Michener and Grimaldi, 1988a,b; Grimaldi *et al*, 1989) suggest that M is an ancient group, possibly Gondwanan (see item *Origin, phylogeny and biogeography*), 100–130 mya old (Michener, 1979; Camargo and Wittmann, 1989 respectively). The other taxa seem to be more recent (Michener, 1990), except possibly B. E is limited to the neotropics (basically in tropical areas), and is presumably post-Gondwanan. A is a typical Indo-Malayan group. Amongst the 9 recent species admitted (*cf* Michener, 1990; see also comments by Alexander, 1991), only 1 occurs in Eurasia and Africa and another in Indo-Malaya and east Asia, the other species, including the most conservative forms (the *dorsata* and *florea* complex; Camargo, 1972; Ruttner, 1988; Alexander, 1991) are found in the Indo-Malayan region up to Timor. Representatives of A are absent in New Guinea and Australia (*cf* Ruttner, 1988; Michener, 1990). Fossil records from Oligocene–Miocene Europe indicate forms that are apparently related to the *A mellifera* group according to Zeuner and Manning (1976); on the basis of forewing morphometric analysis of *Synapis* and *Apis armbrusteri*, Ruttner (1988) suggested approximation with the *Apis dorsata* group. Such taxonomic and distributional patterns might indicate that A is less ancient than M (cf Michener, 1990), and evolved well after the breakup of Gondwana (cf Roubik, 1989), possibly after formation of the Himalayas (it could be hypothesized that *Apis* evolved in isolation in the Indian subcontinent while it was still an island!). Thus, a direct derivation of M from the A or E branch is quite unlikely. B is holarctic (*ca* 250 morphologically homogeneous spp; *cf*

Michener, 1990), with a few species reaching South America (probably a not very ancient migration; *cf* Simpson and Neff, 1985) and mountain areas in the south of the Himalayas. In Africa, it ranges up to the Northern Sahara – fossil forms attributed to the genus *Bombus* have been recorded from the Oligocene–Miocene in palearctic and nearctic regions (Zeuner and Manning, 1976). A relationship with a proto-Bombinae branch is possible if the origin of the Meliponinae in the Laurasian continent is considered, as suggested by Michener (1990).

It is clear that the Apidae complex still remains an *incognita*. The geographic vicariance patterns and fossil record, however, support the hypothesis of greater antiquity for M compared with A, B and E, and that M presents a considerably remote relationship, or possibly no direct relationship with the other Apidae.

## The Meliponinae tribes

Moure (1946, 1951) divided the Meliponinae into the tribes Meliponini Börner 1919 (genus *Melipona*), Lestrimelittini Moure 1946 (genus *Lestrimelitta*, maintaining *Cleptotrigona* apart, since he did not know it *de visu*) and Trigonini Moure 1946 (the remaining genera). Moure (1961:183; Moure *et al*, 1958:491) suppressed the Lestrimelittini, incorporating the genus into the Trigonini.

The genus *Melipona* is exclusively neotropical and, according to Moure (1951), a post-Gondwanan derivative group and so more recent than the main lines of the Meliponinae. Moure (1951, 1961) and Wille (1979b) admitted a cleavage line between the *Plebeia* line and *Melipona*. In the cladogram presented by Michener (1990; fig 6), *Melipona* arises isolated at the base as a sister-group of the other Meliponinae; however, this author recognized (p 92) that this genus is reasonably closely related to *Ple-*

*beia*. Michener (1990:112) suggested the suppression of tribal status for *Melipona*.

### The Meliponinae genera

The outline of modern systematics of the Meliponinae began with the monumental revision made by Schwarz (mainly 1932, 1948) and the comprehensive synthesis by Moure (1951, 1961). A critical revision was presented by Wille (1979b), and some comments were made by Camargo (1989). Recently, a detailed and comprehensive paper was published by Michener (1990), taking into account unknown characters or those not much explored by other authors.

Schwarz (1948) recognized 3 genera for the entire world (*Melipona*, *Lestrimelitta* and *Trigona*, including 18 subgenera). He mainly studied the neotropical and Indo-Malayan fauna. For the neotropical region, Moure (1951) proposed 12 genera and 19 subgenera. In 1961, when he reviewed the old world Meliponinae, he recognized 13 genera for the Indo-Malayan and Australian regions, 10 for the Ethiopian region and 11 genera and 24 subgenera for the neotropics. Finally, in a short note, Moure (1971) proposed an identical approach to that of the old world Meliponinae, elevating all subgenera to generic status. This position was reasserted more categorically by Camargo and Moure (1988) and Camargo (1989).

Wille (1979b) centered his criticisms mainly on Moure's view, and pointed out a new systematic arrangement for the subfamily (8 genera and 14 subgenera, making synonymous 30 of the subgenera admitted by Moure).

Camargo and Moure (1983) proposed the genus *Trichotrigona* for an aberrant form of Meliponinae found in the Amazon. Moure (1989a,b) described *Camargoia* for *pilicornis* Ducke and *camargoi* Moure, 2 divergent forms of the neotropical *Tetragona*

line, and *Sakagamilla*, a monotypic genus, here considered as synonymous with *Scaptotrigona*, since it shows all the autapomorphies of the latter without enough relevant discontinuity to be recognized as an independent clade.

Finally, Michener (1990) suggested for the entire world 21 genera and 17 subgenera (one of them new, *Papuatrigona* Michener et Sakagami, included in *Trigona*), and made synonymous 19 of the general admitted by Moure (table I).

For the fossil forms, the genera *Kelneriapis* Sakagami, 1978 (= *Kelnermelia* Moure in Moure and Camargo, 1978), type species *Trigona (Hypotrigona) eocenica* Kelner-Pillaut, from the later Eocene Baltic amber, *Proplebeia* Michener 1982 type species, *Trigona (Liotrigona) dominicana* Wille et Chandler, presumably from the Oligocene amber, Dominican Republic, and *Meliponorytes* Tosi 1896, type species *Meliponorytes succini* Tosi, from the Miocene Sicilian amber, have been described.

*Trigona prisca* Michener and Grimaldi, the oldest fossil described up to now, 96–74 mya, from Cretaceous New Jersey (USA) amber, was considered to be directly related to *Trigona (s str)* an extant neotropical genus (Michener and Grimaldi, 1988a,b). Such a taxonomic position, however, is dubious (*cf* Camargo and Wittmann, 1989; Michener, 1990:106). Comments on other fossils of recent genera, and some others which had not been completely studied, were provided by Zeuner and Manning (1976), Wille (1977), Moure and Camargo (1978) and Michener (1990).

## ORIGIN, PHYLOGENY AND BIOGEOGRAPHY OF THE MELIPONINAE

The greatest Meliponinae diversity is found in the neotropics (30 supra-specific taxa

**Table I.** Genera and subgenera of Meliponinae admitted by Michener (1990) and after Moure (1961), Camargo and Moure (1988), Camargo (1989) and accepted in the present text. Gen = genus, (SG) = subgenus, syn = synonymous. N = neotropical region, E = Ethiopian region, AU = Australia, NG = New Guinea, MD = Madagascar, I = India, MA = Malayan region.

| Michener (1990) | After Moure (1961) and Camargo (1989) |
|---|---|

*Tetragonisca–Tetragona* Line

| | |
|---|---|
| Gen | *Lestrimelitta* Friese 1903 (N) |
| Gen | *Dactylurina* Cockerell 1934 (E) |
| Gen ( ) | *Trigona* Jurine 1807 (N) |
| (SG) | *Tetragona* Lepeletier Serville 1828 (N) |
| syn | *Ptilotrigona* Moure 1951 (N) *Camargoia* Moure 1989 (N) |
| (SG) | *Geotrigona* Moure 1943 (N) |
| (SG) | *Frieseomelitta* Ihering 1912 (N) |
| (SG) | *Duckeola* Moure 1944 (N) |
| (SG) | *Tetragonisca* Moure 1946 (N) |
| (SG) | *Homotrigona* Moure 1961 (MA) |
| (SG) | *Heterotrigona* Schwarz 1939 (MA) |
| syn | *Platytrigona* Moure 1961 (NG, MA) |
| syn | *Lophotrigona* Moure 1961 (MA) |
| syn | *Tetragonula* Moure 1961 (I, MA, NG, AU) |
| syn | *Tetragonilla* Moure, 1941 (MA) |
| syn | *Geniotrigona* Moure 1961 (MA) |
| syn | Odontotrigona Moure 1961 (MA) |
| syn | *Tetrigona* Moure 1961 (MA) |
| syn | *Trigonella* Sakagami et Moure (in Sakagami 1975) (MA) |
| (SG) | *Lepidotrigona* Schwarz 1939 (I, MA) |
| (SG) | *Papuatrigona* Sakagami and Michener 1990 (NG) |
| Gen | *Trichotrigona* Camargo and Moure 1983 (N) |
| Gen | *Oxytrigona* Cockerell 1917 (N) |
| Gen | *Cephalotrigona* Schwarz 1940 (N) |

*Hypotrigona* Line

| | |
|---|---|
| Gen | *Hypotrigona* Cockerell 1934 (E) |
| Gen | *Pariotrigona* Moure 1961 (MA) |
| Gen | *Lisotrigona* Moure 1961 (I, MA) |
| Gen | *Liotrigona* Moure 1961 (E, MD) |
| Gen | *Trigonisca* Moure 1950 (N) |
| syn | *Leurotrigona* Moure 1950 (N) |
| syn | *Celetrigona* Moure 1950 (N) |
| syn | *Dolichotrigona* Moure 1950 (N) |
| Gen | *Cleptotrigona* Moure 1961 (E) |

*Plebeia* Line and associates

| | |
|---|---|
| Gen ( ) | *Pleibeia* Schwarz 1938 (N) |
| syn | *Mourella* Schwarz 1946 (in Moure, 1946) (N) |
| syn | *Friesella* Moure 1946 (N) |
| (SG) | *Schwarziana* Moure 1943 (N) |
| (SG) | *Scaura* Schwarz 1938 (N) |
| syn | *Schwarzula* Moure 1946 (N) |
| (SG) | *Nogueirapis* Moure 1953 (N) |
| Gen | *Austroplebeia* Moure 1961 (NG, AU) |
| Gen | *Plebeina* Moure 1961 (E) |
| Gen | *Partamona* Schwarz 1939 (N) |
| syn | *Parapartamona* Schwarz 1948 (N) |
| Gen | *Melipona* Illiger 1806 (N) |
| Gen ( ) | *Meliponula* Cockerell 1934 (E) |
| (SG) | *Meliplebeia* Moure 1961 (E) |
| syn | *Plebeiella* Moure 1961 (E) |
| syn | *Apotrigona* Moure 1961 (E) |
| (SG) | *Axestotrigona* Moure 1961 (E) |
| Gen | *Nannotrigona* Cockerell 1922 (N) |
| Gen | *Scaptotrigona* Moure 1942 (N) (n syn *Sakagamilla* Moure 1989) |
| Gen | *Paratrigona* Schwarz 1938 (N) |
| syn | *Aparatrigona* Moure 1951 (N) |

and > 300 described forms) and Indo-Malayan regions (14 supra-specific taxa and *ca* 60 forms). In Africa (10 supra-specific taxa and *ca* 50 forms), Madagascar (1 supra-specific taxon and 4 forms), Australia (2, 8–10) and New Guinea (4, 5), the diversity is much lower.

In this taxon the continental disjunctions are unique within the Apoidea (Michener, 1979), as a result of which a very complex history of vicariance events and great antiquity is presumed. However, there are some obscure points in the taxonomic structure that do not permit a complete reconstruction of the phylogeny of the group. There have been few proposals on the phylogeny (*cf* Moure, 1951, 1961; Wille, 1979b). Michener (1990) presented a cladistic approach suggesting that the Meliponinae originated in North America (West Laurasia); nevertheless, there is a certain difficulty in accepting the model, in view of some taxonomic problems.

To analyze the hypothesis on the geographic origin of the Meliponinae and the possible sequence of events determining the present disjunction pattern, it is necessary to first clarify some questions on the relationships among the taxa: which groups can be recognized as sister-groups?

Moure (1951, 1961) proposed at least 3 main phyletic lines, *Tetragonisca–Tetragona*, *Plebeia* and *Hypotrigona*, present in several continents, based principally on the character form of the micropilose structure (= keirotrichia; Michener, 1990) of the inner surface of the hind tibia of the workers.

### The Tetragonisca–Tetragona *line*

Michener (1990: 87, character 4), questioned the polarity of this character state. However, he considered elevated and narrow keirotrichia, restricted to the median longitudinal band, leaving a broad bare (or with sparse bristles) depressed posterior margin, as an apomorphic state (Moure, personal communication) consider it primitive or plesiomorphic), and suggested the Malayan *Trigona* (*sensu* Michener) as a sister-group of the neotropical *Trigona*. This character state is present in *Trigona (s str)*, *Tetragona*, *Frieseomelitta*, *Geotrigona*, *Duckeola*, *Tetragonisca*, *Ptilotrigona*, *Trichotrigona*, *Camargoia*, *Oxytrigona* and *Cephalotrigona* from the neotropical region and in *Homotrigona*, *Heterotrigona*, *Platytrigona*, *Lophotrigona*, *Tetragonula*, *Tetragonilla*, *Geniotrigona*, *Odontotrigona*, *Tetrigona*, *Trigonella* and *Papuatrigona* from the Malayan region and the eastern Indian subcontinent (*Platytrigona* ranges as far as New Guinea; *Tetragonula* ranges as far as the Solomon Islands, Caroline Islands, New Guinea and northeastern Australia; *Papuatrigona* is restricted to New Guinea). In Africa, only *Dactylurina* presents such a

state. In the fossil forms, it is present in *T prisca* (Michener and Grimaldi, 1988a) from the nearctic region and in *Tetragonula devicta* from Burma (*cf* Kerr and Maule, 1964; Wille, 1977; Moure and Camargo, 1978). This grouping as proposed by moure (1961), was regarded by Michener as a single genus, *Trigona*, from which only *Oxytrigona* and *Cephalotrigona* were excluded, being considered as specialized genera associated to the clade. He also excluded *Dactylurina*, which, in spite of presenting this character state and others in common with the *Trigona* line (*eg* plumose hairs along the posterior margin of the hind tibia, and an area in the hind basitarsus of *D staudingeri*, similar to the sericeous area of the *Trigona*), is considered by Michener (1990), to be closely related to *Plebeina*, another phyletic line from Africa, based on the male and worker gonostylus form and male gonocoxyte.

Other characters, such as the sericeous area on the base of the inner surface of the hind basitarsus of the worker (a well defined area of dense micropilosity), place the Indo-Malayan groups of *Trigona (sensu lato)* line, except *Lepidotrigona*, *Homotrigona* and *Papuatrigona*, directly as a sister-group of *Tetragonisca* and *Trigona (s str)* from the neotropical region. However, this character can be plesiomorphic for *Trigona (s lat)*. A sericeous area is also present in the fossil *T prisca*. In addition to this character, *Tetragonisca angustula* Latreille has a structure interpreted as the 8th metasomal sternum (Camargo, *in litt*), which also indicates a plesiomorphic condition.

### The Plebeia *line*

This line is poorly defined and the relations among included taxa are obscure and doubtful. According to Moure (1951), this line includes the groups that have enlarged

keirotrichia, leaving only a narrow posterior margin, depressed or not. They are as follows: from the neotropical region, *Plebeia (s str)*, *Mourella*, *Friesella*, *Schwarziana*, and the associated genera *Melipona*, *Scaura*, *Schwarzula*, *Partamona*, *Parapartamona* and *Nogueirapis*, and possibly more remotely derived *Paratrigona–Aparatrigona* and *Nannotrigona–Scaptotrigona*; from the Ethiopian region, *Plebeina*, *Plebeiella* and *Meliplebeia*, and from Australia and New Guinea, *Austroplebeia*. Michener (1990) nevertheless, did not consider these African and Australian taxa as sister-groups of the neotropical groups; for the African forms he suggested a relationship with neotropical *Trigonisca (s lat)* and *Hypotrigona* from Africa. Michener had good reasons for excluding some African groups from a direct relationship with *Plebeia*. Loss of the rastellum and presence of a well-developed posterior parapenicillum are clear synapomorphies linking *Meliponula*, *Plebeiella*, *Meliplebeia*, *Axestotrigona* and *Apotrigona* without corresponding forms in other continents, so that he considered them to belong to a single genus: *Meliponula*. The inclusion of *Hypotrigona–Liotrigona* in this clade seems logical, since the modifications in the rastellum (soft hairs) and posterior parapenicillum, are similar to that of *Meliponula* (*sensu* Michener). On the other hand, contrary to Michener's interpretations, *Plebeina* presents a functional and well developed rastellum and an undeveloped parapenicillum, exactly like those of *Plebeia (s str)*. Unless this character (rastellum) arose by reversion or *de novo* (which is perfectly possible, since it is only a comb of modified setae), such a feature could indicate a relationship between *Plebeina* and neotropical forms (Michener codified rastellum as weak or absent in *Plebeina*, *Austroplebeia*, *Dactylurina* and *Trigonisca s lat*; nevertheless, it is present and functional in all of them). Other characters linking the African forms (including *Dactylurina* and *Plebeina*) with the exception of *Hypotrigona*, are the gonostyli in workers, enlarged and diverging apically and covered with micropilosity. Michener (1990:88, characters 11, 12, 13) considered the worker gonostyli to be well separated at the base, converging apically and covered with abundant long bristles and with absence of micropilosity, as plesiomorphic states. We are of the opinion that the polarity of the latter character (0 = micropilosity absent; 1 = present), is improbable. If it is considered that reduced sting without biological function is not subjected to selective pressure at least theoretically, it therefore should not acquired new attributes only to suffer reduction or loss of structures (unless it is supposed that reduction of the sting occurred at least twice independently in ancestors of the Meliponinae). In this way, bristles and micropilosity would appear in combination in the ancestor (loss of micropilosity and bristles might occur independently). This combination association to cylindrical and convergent gonostyli, in our view, occurs in *Trigonisca*, (*s lat*, *cf* Michener, 1990; figs 38, 39), from the neotropical region, and indicates an approximation to *Plebeina*, if it is also considered that both have a well developed and functional rastellum. Although the relationships between the African and neotropical taxa are still unclear, Michener (1990) also recognized a closer relationship between them, rather than with any other taxon from other continents.

Among the neotropical taxa associated with the *Plebeia* line certain problems also arise. According to the characters considered by Michener (1990), *Melipona* arises at the base as an isolated branch, a sister-group of the other Meliponinae. The acute submarginal angle in the forewing constitutes the main synapomorphy that separates *Melipona* from the *Plebeia* branch and associated taxa; this, however, is a difficult

character to codify. An acute angle (= 75°) occurs in some species of *Paratrigona* (another plesiomorphic character in this genus is the presence of the 2 submarginal cells, which are very well delimited in some species; *cf* Camargo and Moure, 1992), while in *Melipona*, in some forms of the *marginata* group, this angle is practically at a right angle (85–90°). Some doubts about the form of the male genital capsule (rectigonal, schizogonal) also remain, *eg* the schizogonal condition of *Melipona* also appears, according to Michener (1990) in some other taxa such as *Nannotrigona*. Reevaluation of these characters could bring *Melipona* much nearer the *Plebeia* branch, or even place it as a derivative group of the *Plebeia* stock. On the other hand, *Plebeia (s str)*, even taking into account some of the characters considered by Michener (1990), seems to be a derivative form. For example, the median apical process of the 6th metasomal sternum of the male (a plesiomorphic state, *cf* Michener, 1990:88), present in most of the other taxa, including *Mourella* (considered synonymous with *Plebeia s str* by Michener, 1990), is absent in *Plebeia (s str)*. Moreover, *Mourella* exhibits a set of other bionomic characters associated with subterranean nesting habits (simple nest entrance, not delimited by resin or cerumen, gallery between the surface and the nest not lined with cerumen, listed among others by Camargo and Wittmann, 1989), considered by us as plesiomorphic states.

For *Austroplebeia*, the problems are just as numerous. In the cladograms of Michener (1990), it appears related to derivative African forms, mainly because of the way in which the characters were codified, particularly the main synapomorphy, rastellum absent. On the contrary, *Austroplebeia* has a well developed and functional rastellum, as in neotropical *Plebeia (s str)*. Taking into account male genital characters, with the exception of the absence of

spatha, even Michener (1990) recognized an approximation to neotropical forms. Furthermore, other characters such as unmodified pregenital sterna and the 6th metasomal sternum with a median apical process in males, general body form, triangular hind tibia, enlarged keirotrichia, and rastellum present in workers are suggestive of a relationship with the neotropical *Plebeia* line, primarily *Mourella*. It is less probable that such a combination of character states, even if they are considered as plesiomorphic states, is present in unrelated taxa (see also Camargo and Wittmann, 1989) or arises convergently, as suggested by Michener (1990:104); there is no known determinant factor of convergence for such a set of characters. With reference to the sting structure of *Austroplebeia*, cylindrical gonostylus, covered with micropilosity and setae (or bristles) are plesiomorphic states and are also present in neotropical forms *(Trigonisca)*. In fact, in our opinion *Austroplebeia* does not share apomorphies with any other taxa, but exhibits a series of plesiomorphic states, resembling neotropical forms rather than African forms.

Fossils related to *Plebeia (s str)* have been described from the Oligocene Amber, Chiapas, Mexico (*Nogueirapis silacea* Wille, 1959) and from the Oligocene Amber of the Dominican Republic (*Proplebeia dominicana*; *cf* Michener, 1982).

### The Hypotrigona *line*

This line includes *Hypotrigona (s str)* and *Liotrigona* from Africa, *Trigonisca, Leurotrigona, Celetrigona* and *Dolichotrigona* from the neotropical region, and *Pariotrigona* and *Lisotrigona* from Indo-Malaya. These are the smallest Meliponinae known (ca 2.0 mm) and, according to Moure (1961), most of the characters considered could indicate convergence associated with reduc-

tion in body size rather than phylogenetic relationships. In Michener's cladograms they appear as related taxa, with the exception of *Liotrigona*. According to Michener (1990), the long malar space, nearly right-angled submarginal angle and bristles arranged in successive transversal rows on the inner surface of the hind basitarsus of *Pariotrigona* suggest some species of the neotropical *Trigonisca (s lat)*. Males of *Pariotrigona* which might corroborate or refute such a relationship, are not known.

Fossils, possibly related to *Hypotrigona (s lat)*, have been described from the Eocene Baltic Amber (*Kelneriapis eocenica*; cf Moure and Camargo, 1978; Sakagami, 1978) and from the East African Copal (*Hypotrigona gribodoi*, cf Wille, 1977). *Liotrigona vetula* was described by Moure and Camargo (1978) from a Copal piece of unknown age and origin.

An analysis of all taxa, taking into account the biogeographic regions, allows the following relationships to be suggested:

– Between neotropical and African regions there are no defined sister-groups, but indications of possible relationships among *Plebeina*, *Plebeia* line and *Trigonisca (s lat)* and between *Hypotrigona* and *Trigonisca (s lat)*, as suggested by a still confused combination of plesiomorphies and apomorphies. The conspicuous divergence of the remaining African taxa and the absence of representatives from the *Tetragonisca–Tetragona* line (except possibly *Dactylurina* as a relict form) in Africa indicate, according to Michener (1990:97), that the African fauna must have evolved in substantial isolation from African and Eurasian invasions.

– Between the neotropical and Malayan regions, the relationships are more clearly defined by the presence of sister groups from the *Tetragonisca–Tetragona* line (*Trigona s lat*) and also by possible relationships between *Trigonisca (s lat)* and *Lisotrigona* and *Pariotrigona*.

– Between the neotropical region and Australia and New Guinea, there is no defined sister-group, but indications of a close relationship between the *Plebeia* line and *Austroplebeia* exist.

– Between the African and Malayan regions, sister-groups do not occur. There are only indications of a relationship between *Hypotrigona* and *Pariotrigona*. In the Malayan region there are no forms related to the *Plebeia* line. Between Africa and Australia, there is no sister group.

– From the Malayan taxa, 3 genera occur in New Guinea and only 1 in Australia. *Austroplebeia* only occurs in New Guinea and Australia.

The hypothesis suggested by Michener (1990) of an origin in North America (West Laurasia) seems well sustained in his cladograms (figs 6, 7, 8) and in the fossil record *(T prisca)*. He suggested that the present vicariance pattern in the Meliponinae results from a distribution throughout the holarctic region which took place when this area was warmer. He considered the discontinuity between the neotropical and African fauna as indicative that the Meliponinae from North America reached South America after considerable separation between the latter and Africa, and that the African fauna evolved when Africa was substantially isolated from American and Eurasian invasions. On the other hand, the indication of a relationship between *Austroplebeia* from Australia and the *Plebeia* line from the neotropical region rather than with African forms, and the absence of forms related to this group in the Indo-Malayan region, are suggestive of a panaustral migration route *via* Antarctica (Camargo, 1989; Camargo and Wittmann, 1989). This pattern is indicative of the presence of the Meliponinae in Southern South America; at least between the Upper Cretaceous and

the Early Tertiary. Also, the presence of *Plebeia* line forms restricted to southern Brazil, especially *Mourella*, as previously discussed, suggests the origin of this group (*Plebeia* line) in the southern south-American cratons (Camargo, 1989, 1990; Camargo and Wittmann, 1989). This possible antiquity of the *Plebeia* line (a basic branch in the cladogram of Michener, 1990) in South America, and the indication of a more remote relatonship between the neotropical and African taxa (*cf* Michener, 1990), as already discussed, are suggestive that a West Gondwanan origin for Meliponinae is also a plausible hypothesis (Camargo, 1989, 1990; Michener, 1979; Roubik, 1989). Thus, the Malayan and Australian taxa would be derived from the neotropical stock, possibly after the split from Africa.

The presence of sister-groups from the *Tetragonisca–Tetragona* line in Malayan and neotropical regions, and absence of related taxa in Africa suggest an ancient connection track, *via* the holarctic region, before the separation of West Eurasia and North America, and before the formation of the immense Himalayan mountain range by the collision of India with Asia, a remarkable barrier to recent fauna. The presence of fossils from the Upper Cretaceous in New Jersey, USA (*T prisca*, related to *Tetragonisca–Tetragona* line) and from the Eocene Amber Baltic (*Kelneriapis eocenica*, related to *Hypotrigona* line) are possible indications of this migratory route. An ancient communication between South and North America, *via* the proto-Caribbean arc, in the Early Tertiary (Camargo *et al*, 1988) or in the Upper Cretaceous, has been proposed for bees and other fauna (*cf* Savage, 1983; Rage, 1986; Guyer and Savage, 1987; Roubik, 1990; see also the literature in Savage, 1991). The neotropical *Tetragona–Tetragonisca* group has its greatest diversity and dispersal center at the Guyana and northern Brazil shields.

India, in isolation for a long period (*cf* literature in Patterson and Owen, 1991) possibly did not participate in the dispersal of the Meliponinae, and was invaded later by Malayan *Trigona (s lat)* (this would explain the presence of only about 5 species on eastern India). The invasion of New Guinea and Australia by *Trigona (s lat)* taxa of the Malayan region seems to be much more recent.

The hypotheses of Kerr and Maule (1964), who supposed that the Meliponinae originated in South America and migrated to North America during the Eocene, and *via* the Bering strait to other continents, and that of Wille (1979b, 1983) who suggested an African origin in the Upper Cretaceous–Lower Tertiary, and migration to Europe during the Tertiary, and from there to the other continents, are not supported, in view of recent evidence on the antiquity of this group and relationships among the taxa.

## ACKNOWLEDGMENTS

**Résumé — Systématique, phylogenèse et biogéographie des *Meliponinae* (Hymenoptera, Apidae) : synthèse.** Dans cet article de synthèse sont discutées les principales propositions concernant la systématique, la phylogenèse et la biogéographie des Meliponinae, ainsi que la polarité et l'importance de quelques caractères morphologiques. Bien que tout un ensemble de synapomorphies (par ex les corbicules, le *rastellum*, l'articulation du basitarse postérieur près de l'extrêmité antérieure de

l'apex du tibia) suggèrent que les Meliponi-
nae constituent un groupe cophylétique
des Apinae, des Bombinae et des Euglos-
sinae, leurs relations avec ces sous-
familles restent floues. Leur répartition gé-
ographique (Meliponinae : zone pantropi-
cale; Bombinae : zone holarctique; Euglos-
sinae : zone strictement néotropicale;
Apinae, principalement indo-malaisienne)
et les données des fossiles indiquent un
âge très ancien pour les Meliponinae (le
plus vieux fossile, *Trigona prisca*, prove-
nant de l'ambre du New Jersey, USA, est
daté du Crétacé, soit 96-74.10$^6$ ans) et
suggèrent une origine indépendante ou
une divergence très précoce d'une bran-
che des proto-Apidae. L'interprétation de
certains caractères (par ex rastellum, kei-
rotrichia, angle submarginal de l'aile anté-
rieure), présentée dans une analyse cla-
distique récente (Michener, 1990), est
discutée. Une autre polarité pour les carac-
tères de l'aiguillon est suggérée (0 = go-
nostyle avec micropilosité abondante, 1 =
micropilosité absente). L'absence de repré-
sentants semblables à *Plebeia* en Indo-
Malaisie et des indications selon lesquelles
*Austroplebeia* (d'Australie) est étroitement
apparentée à la lignée *Plebeia* des néotro-
piques (dont les centres de diversité et de
dispersion sont situés dans les boucliers
du Brésil méridional) suggèrent l'existence
d'une voie de liaison panaustrale et la pré-
sence de Meliponinae en Amérique du
Sud au moins entre le Crétacé supérieur et
le début du Tertiaire. Les relations phylo-
génétiques probables et la répartition géo-
graphique laissent à penser que l'origine
gondwanienne occidentale des Meliponi-
nae est une hypothèse plausible. Les rela-
tions de groupes sœurs entre les taxons
de Malaisie et la lignée *Tetragona–
Tetragonisca* (dont les centres de disper-
sion et de diversité se situent dans les
boucliers des Guyanes et du Brésil septen-
trional), telles que les indiquent certaines
synapomorphies, et une relation possible

entre *Trigonisca (s lat)* et *Lisotrigona* et
*Pariotrigona* suggèrent une liaison ancien-
ne, peut-être du Crétacé supérieur, à tra-
vers la région holarctique. Les formes fos-
siles du New Jersey et d'Eurasie (ambre
de la Baltique) sont une preuve éventuelle
de cette route de migration. L'Inde n'a vrai-
semblablement pas pris part à la disper-
sion des Meliponinae et n'a été colonisée
que plus tard à partir de la Malaisie.
L'absence de représentants de la lignée
*Tetragona–Tetragonisca* en Afrique et la
grande divergence des taxons présents
sur ce continent indiquent une longue pé-
riode d'isolement. Néanmoins des relations
plus étroites avec les taxons néotropicaux
(lignée *Plebeina–Plebeia* et *Trigonisca s
lat*, *Hypotrigona* et *Trigonisca*) qu'avec tout
autre taxon des autres continents sont
suggérées par une combinaison confuse
de plésiomorphies et d'apomorphies.

**systématique / biogéographie / phyloge-
nèse / Meliponinae / Apidae**

**Zusammenfassung — Systematik, Phy-
logenie und Biogeographie der Melipo-
ninen (Hymenoptera, Apidae): Eine
Mini-Review.** In dieser Übersicht werden
die wichtigsten überlegungen zur Systema-
tik, Phylogenie und Biogeographie der Sta-
chellosen Bienen, sowie die Polarität und
Bedeutung einiger morphologischer Merk-
male diskutiert. Obwohl eine ganze Reihe
von Synapomorphien (zB Corbicula, Ra-
stellum, Artikulation des hinteren Basitar-
sus nahe dem vorderen Ende der Tibia-
spitze) die Einordnung der Meliponen als
co-phyletische Gruppe mit den Apinen,
Bombinen und Euglossinen nahelegt, blei-
ben doch die Beziehungen zu diesen Un-
terfamilien unklar. Geographische Vertei-
lung (Meliponinen – pantropisch, Bombi-
nen – holarktisch, Euglossinen – streng
neotropisch, Apinen – vorwiegend indo-
malayisch) und fossile Funde deuten auf

ein größeres Alter der Meliponinen hin (das älteste Fossil, *Trigona prisca*, aus einem Bernstein aus New Jersey, USA, 96-75 $10^6$ Jahre) und lassen einen unabhängigen Ursprung oder eine frühe Abzweigung von einem Ur-Apidenzweig vermuten. Die Interpretation einiger Merkmale in einer kürzlich publizierten kladistischen Analyse der Meliponinen (Rastellum, Keirotrichia, submarginaler Winkel des Vorderflügels) wird diskutiert. Außerdem wird eine andere Polarität von Stachelmerkmalen vorgeschlagen (0 = Gonostylus mit reichlicher Mikropilosität, 1 = Mikropilosität fehlend).

Die Abwesenheit von *Plebeia*-ähnlichen Vertretern in Indo-Malaya und die Verwandtschaft als Schwestergruppen von malayischen und neotropischen Meliponinen (die Linie *Tetragona–Tetragonisca* und möglicherweise *Trigonisca–Pariotrigona, Lisotrigona*) so wie die mögliche Verwandtschaft zwischen *Austroplebeia* und der neotropischen *Plebeia*-Linie legen einen panaustralischen Verbindungsweg und einen weiteren über die holarktische Region (möglicherweise in der oberen Kreide) nahe. Die Anwesenheit von meliponinen im südlichen Südamerika (mindestens zwischen der oberen Kreide und dem frühen Tertiär) ist wahrscheinlich. Diese phylogenetischen Beziehungen und Ausbreitungsmuster machen die Hypothese eines Ursprungs der Meliponen aus West-Gondwana plausibel. Fossile Funde in New Jersey, USA, und Eurasien (Baltischer Bernstein) sind mögliche Beweise für diese Wanderungsrouten. Indien war wahrscheinlich an diesen Ausbreitungswegen nicht beteiligt, sondern wurde erst später von Malaya aus besiedelt. Das Fehlen der *Tetragona–Tetragonisca*-Gruppe in Afrika und die große Divergenz der auf diesem Kontinent vorhandenen Taxa weisen auf eine lange Isolationsperiode hin. Es bestehen jedoch Hinweise einer näheren Verwandtschaft zu den neotropischen Taxa (*Plebeina-Plebeia*-Gruppe und *Trigonisca, sensu lato*: *Hypotrigona* und *Trigonisca*), nahegelegt durch eine verwirrende Kombination von Plesiomorphien und Apomorphien, als zu Gruppen von anderen Kontinenten.

**Systematik / Biogeographie / Apidae / Meliponinae / Phylogenie**

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