11. Why do they keep changing the names of our stingless bees (Hymenoptera: Apidae; Meliponini)? A little history and guide to taxonomy

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Abstract

Bee taxonomy and identification methods are discussed and put within a context of biology and accessible data. Some fundamentals in type specimen collection and use, and their description, are outlined. The reasons for shifting or overturning previous classification and identification are illustrated with examples from Neotropical bees. Keys are given note as good justification for training taxonomists, but keys are, inevitably, often incomplete when considering species. The current status of the tribe Meliponini is that at least 56 genera are recognized and used. The use of small defined groups, whether genera or subgenera, is important to permit an advance in study and collection of stingless bees. Whether the future classification will incorporate subgenera or primarily genera is an open question.

Keywords: bee taxonomy, field work, museum research, stingless bees

Introduction

Taxonomists are trained to place organisms in their place, including other taxonomists. Sometimes I wonder why the road to good taxonomy is so full of obstacles and mistakes? And what is good taxonomy? Recognizing species is certainly the heart of this pursuit, and taxonomy influences biology, just as biology renews taxonomy. That process cannot stagnate. Yet, many practitioners of biology, whether applied or academic, seem ignorant of what is accomplished with good taxonomy, how it is done, and why it is done to preserve and improve order in this complex and ever-threatened biological world.

1.1 Tracking down species

While we wonder if published keys are sufficient to appreciate the variety among stingless bees found in tropical wildlands, it seems likely that the last thing we might reasonably expect is a fully functional key for stingless bees in any major region. We have solid foundations for larger units, such as genera (Michener 2007; Silveira, Melo and Almeida 2002; Hanson and Gauld 1995) while the smaller units, both biological and geographical, have few satisfactory works. They are generally susceptible to many errors and omissions. We have no reason to suppose that one large key can be produced, with the result that all species will be assigned valid names, without considerably more effort. Meanwhile, and likely in perpetuity, this fact amply justifies support for taxonomists. They will do the commendable jobs of tracking down species, and aligning their nomenclature with biology and history.

In the tropics, where possibly 20% of species coming from studies of true wildlands are ‘new’, a rather fine grade of preliminary taxonomy is
appropriate. From my experience with collections, certainly throughout the tropics, an initial sorting to a small group, even when the species name is uncertain, is considerably more efficient than placing a specimen in the *Trigona* (vide Schwarz 1948) or Trigonini (Moure 1946, now an obsolete tribal term). At one time (Moure 1951; Wille 1983) the meliponines were discussed as subfamily *Meliponinae*, with, to varying degree, tribes *Meliponini* Lepeletier, 1936 (Camargo and Pedro 2013), Lestrimelitini Moure, 1946, and Trigonini Moure, 1946 including all the world’s species. After 1990, the Meliponini were considered a single tribe containing all stingless honey-making bees, and one subfamily, Apinae, containing these and the bumble bees, honey bees, and the euglossines (Michener 1990, 2007, 2013). Bees have seven families, widely accepted (Engel 2011). There are also somewhat confusing informal designations of species names, such as *Trigona aff. corvina*, or *Meliponula* cf. *nebulata*. This kind of taxonomy arises normally by correctly following a key to its end, and coming up with something that does not exactly match the species named there. This puts the observer in the fix of what to do. I often find myself, in Panama, when told that a place I am seeking is ‘next to Juan’s house’. I can say, with complete justification “How should I know where Juan lives?” Sometimes an entire group of species is given an informal name, such as the *Melipona fasciata* group, or the *Trigona fuscipennis* group, in place of a formally defined group, like genus or subgenus. I see limited use for informal groups, because they are not well defined (but are best viewed as approximations).

From where we now stand, there is an incredible information age, where search engines are used (e.g. Google, Discover Life, ITIS, and Wikipedia— the last not extensively reviewed or subject to wide scrutiny before web-publication). Therefore, there are a mix of statements that might well be authoritative and unassailable, there are opinions, and there are mere guesses. Taxonomy, among themes pursued below, also contains the same three elements. Nonetheless, on the web one can locate a name and find details of where a species came from, the description and taxonomic authority, and when it first appeared in print. This lessens the need for each species name given in a journal publication to carry along with it the taxonomic authority and original date of publication, as currently required in many biological publications. On the other hand, because tropical reference specimens in museums include those collected during the 18th and 19th centuries, and the upkeep or curation of specimens in museums— particularly in the face of economic stress— has faltered, the whereabouts of the type specimens or type series may be unascertainable, or the specimens in question dirty, broken and fairly useless. (A type specimen, by the way, is a critical reference material— one to which all other material is compared, to determine whether or not they are the same thing.) Type reference specimens, or their designated replacement specimens collected from the type locality (see, e.g., Rasmussen and Michener 2010) are valuable because fine details or even natural dimensions, shape or color are often lacking in the old catalog-style taxonomic literature, however well illustrated, and in other scientific publications.

In summary, scientific names may be valid, because they were published in an accessible journal, but often the original description was not clear enough to resolve confusion over similar species, the original material is unavailable or of little use, or both. As many are aware, this is still far better (having a valid name applied to a specimen recorded in a particular time and place) than deciding among a list of common names, many applied to multiple species, and some applied to species for which other common names also are used. However, both cases, and particularly the latter, also occur, over and over, with scientific names. (I will not address the obvious problem that specimens are often plainly identified incorrectly, particularly by non-specialists.) Why does this happen?

### 1.2 The ghost of taxonomy past

Confusion as to nomenclature, bookkeeping and philosophical turnover occur not because whoever was in charge was ‘on holiday’ when that specimen or its name appeared in their museum or journal. It is because Nature is diverse, libraries do not have all the journals ever published, nor are all journals read and understood by everyone. Most species usually require additional study, in order to define their natural variation, geographic range and the diagnostic boundaries between them. Not least of all, people do require some time to make up their minds. When, for example, the British Museum’s Entomological Collection was moved into a new building in 1965, that collection was still referred to as being at the British Museum, until officially renamed the Natural History Museum, in 1990 (Fortey 2008). The same thing happens with biological specimens that have been relocated to different groups or viewed with different principles of classification. After *Trigona jaty* was renamed *Tetragonisca angustula* (Moure
1946, 1971), it required some time before the change was universally accepted (see Vit, Pedro and Roubik 2013). *Trigona carbonaria* was changed to *Tetragonula carbonaria* (see Rasmussen 2008), but the former persists in the literature (present volume).

People, including taxonomic authorities, do make mistakes. My first and likely worst taxonomic mistake (Roubik 1980) was a failure to notice that a bee I published as a new species already had a name, given to it by Fabricius in 1798. I was in good company, however, because T. D. A. Cockerell made the same mistake, in 1920 (see *Friesomelitta flavicornis*, in Camargo and Pedro 2013). In later field work, I discovered a biologically unique stingless bee in Panama that obtained protein only from rotting flesh (Roubik 1982). That ‘vulture bee’ I had thought was *Trigona hypogea*, described by Silvestri in 1908 and noted for its distinctive morphology by Schwarz (1948). It was an undescribed species, present only in Panama and Costa Rica. Camargo and Roubik published most of this information in 1991.

Fossil bees are an exciting way to become familiar with stingless bees, because several species are found in Dominican and Chiapas amber, roughly 20,000,000 years in age (Camargo, Grimaldi and Pedro 2002; Engel 2004). Moreover, there are not just a few, badly deformed examples; thousands of complete bee specimens are available for study, even in single chunks of amber.

Alvaro Wille (1959) and Wille and Chandler (1964) describe the first stingless bee in amber from the Neotropics. Michener (1982), then Camargo et al. (2002) and recently, Engel (2004) change the use of names regarding those bees, I will make another contribution here, and Engel and Michener (this volume) will have the last word. Wille’s *Nogueirapis silacea*, the fourth known species of *Nogueirapis* (Moure and Camargo 1982) and the only fossil one, has a holotype and at least one paratype. Wille’s publication contains drawings from each, including a view of the metatibia. It has a narrow, flattened and smooth margin running its length. That is not characteristic of *Nogueirapis. Proplebeia dominicana* (Michener 1982) replaced the *Trigona (Liotrigona) dominicana* name given by Wille and Chandler (1964) and conveys the Neotropical (*Plebeia*-like) resemblance, and also place of discovery, of the Dominican amber *Proplebeia*. Something like this genus is in fact also found in Chiapas amber (M.S. Engel, personal communication). When *Nogueirapis silacea*, as originally described in the literature, and the very clear hind leg drawing among the four presented, were reviewed by Camargo et al. (2002) those authors changed the genus name to *Proplebeia*. Engel (2004) overturned this change in genus, finding that the holotype is not *Proplebeia*, but I found that at least one paratype is certainly not *Nogueirapis*. It was shown to me by P. Hanson, retained at the University of Costa Rica. Thus, the type specimens were not only different species, but different genera, one extinct and one evidently still living. This is not an impossible situation, only rare. I have seen a similar misclassification of *Meliwillea as Oxytrigona* by Schwarz (Roubik, Lobo and Camargo 1997). From the foregoing examples, one can appreciate that there are inevitable weak points in the chain of conclusions drawn on one side from nature, and on the other from collections and published records. When more information is sought and careful analysis is made, they are corrected.

Another problem occurs when, for various reasons, a name appears in print, but a formal description has not previously been published. This is true of *Trigonisca rhodoptera nomen nudum* (which means it has no name), a meliponine bee found only in a small part of Costa Rica. A very similar *Trigonisca* commonly called *T. buyssoni* also occurs there (D. W. Roubik, unpublished). *Trigonisca buyssoni* is, in reality, absent in Central America (Camargo and Pedro 2013). Both bees are without scientific names, because no one has described them and published this in an accessible journal. They have no common names either, save perhaps ‘chupa-ojos’, or similar monikers given to all tiny meliponines that like drinking vertebrate sweat or even tears (Roubik 1996; Bänziger and Bänziger 2010).

Similar taxonomic errors come to light, perhaps the bulk of those left for taxonomists to ponder and correct, as synonyms —names that are given but do not apply to a taxon in question. The reason is most often one of priority—one older published name exists and therefore has priority, unless there are compelling reasons, such as widespread use and economic value, to continue using the ‘wrong’ name (Camargo and Pedro 2013). Michener (1995) found this situation with the name *Aphanuera*, a name previously given to genus *Trigona*, in the early 1800s, by Gray. A more recent name for a species that already has a name is called a ‘junior synonym’, as is *Trigona (Tetragona) savannensis* (Roubik, 1980) for *Friesomelitta flavicornis* (Fabricius, 1798).

Another kind of error, found in stingless bee literature, is assignment of one name to the worker and another to the male. This occurs because only
males or only workers were originally available, and there was later no compelling reason to consider them of the same species (without taking a sample from a single nest). This happened with *Trigona muzoensis* (described as a male), which is the same species for which workers were later called *Trigona pallida* or *T. pallens*. The male was later collected, along with nesting information, to establish the species status of *T. ferricauda*. *Trigona ferricauda* and *T. muzoensis* (= Central American bees formerly called *T. pallens*) coexist in the same forests and, by current classification of this status (see Moure and Kerr 1950) cannot be the same species. I verified this by comparing the type male or worker to those collected from nests in Panama, where I obtained both males and workers. The nests, too, differed in their architecture and habit (Roubik 2006). *Trigona muzoensis* and *T. ferricauda* nest in the occupied nests of termites, while *T. pallens*, resident only to South America, lives in tree cavities. Some *Trigona*, however, appear to both use cavities and build exposed nests (Rasmussen and Camargo 2008). Finally, there is substantial momentum in following certain ‘schools’ in taxonomy, and one outcome is that the name or classification given by one proponent is blithely ignored by the contrary proponent. One particular *Trigona*, widespread in both South America and Central America, and reaching southern Mexico, has been called both *Trigona silvestriana* and *T. amalthea* (Moure 1960; Roubik 1992; Rasmussen and Camargo 2008; Roubik and Moreno 2009; Ayala et al. 2013). I went to the Paris Museum of Natural History three times to compare the types of *T. silvestriana* with bees I had found from Mexico to Brazil. It was a special problem because there are more than one species among the types of *silvestriana* sensu Ayala et al. 2013, which were collected in different countries, and now deposited in the Museum of Natural History in Paris (Moure 1960 and personal observation). Almost the entire type series I saw was from South America, and all were considerably larger than similar bees, few included in the museum ‘cotypes’ or ‘type series’ from Central America. Nonetheless, Schwarz (1948) decided that the single, definitive type of *Trigona silvestriana* Vachal, 1908, would be that collected in Honduras, after carefully considering the many opinions expressed in the literature. The remaining type series bees, including one male, from South America, were not the same as that Honduran species. Furthermore, Moure (1960) made additional comparison of *T. trinidadensis* and *T. amalthea*, stating they were the same bee, in agreement with past authors who made various comparisons (Lepeletier, Silvestri, Friese, Ihering, Ducke and Mariani), and with Camargo and Pedro (2007), who list *Melipona trinidadensis* (Provancher 1888) as a synonym of *Trigona amalthea*. I might agree, because this bee is the only large *Trigona* that I knew in Central America, Trinidad and Mexico. However, it now seems that the very similar large, black *Trigona* in Costa Rica, and those in Panama, are two different species (D. W. Roubik, unpublished). It was not only *Trigona silvestriana*, making this a difficult case of crypsis, which Rasmussen and Camargo (2008) encountered in their molecular information on the large, black *Trigona* with uniformly colored dark wings. Moure wrote (op. cit. 1960) that the original description of *T. amalthea* by Olivier, in 1798, corresponded to *T. trinidadensis*, which was a much older description than that of currently accepted *T. silvestriana*. That description states it is a small bee (it is not) and it has mostly clear wings (it does not), and Moure gives the forewing length as 10.6 mm, far greater than *T. trinidadensis*, *T. silvestriana*, *T. amalthea* or its probable synonym *T. fusciennis* (Friese, 1900). Moure (1960) in agreement with Schwarz (1948) believed the name ‘available’ for *amalthea* was *fusciennis*. Because Schwarz was guessing, and never actually saw the type he made represent *T. silvestriana*, and Moure was guessing that a type of *T. amalthea* would be found in the Kiel Museum (it is currently elsewhere, Camargo and Pedro 2013) both the foregoing arrangements appear very questionable. We have a difficult situation—compounded by the fact that the type of *T. amalthea* was claimed to be collected in French Guiana, where no such a large, dark bee has been found in many years or can be in any way confirmed to have come from there (Schwarz 1948; Moure 1960; Pauly et al. 2013). It probably really is a smaller bee, similar to *T. fusciennis*, but not that species. A mislabeled specimen, a ‘ghost’ type, and a fairly inaccurate description by both Olivier (1908) and Vachal (1798), all are connected with a single stingless bee—not just any stingless bee, but one of the larger and more common bees in Neotropical forests. It is foraging in my kitchen right now, and I think it’s probably called *T. trinidadensis*.

1.3 The present future of stingless bee taxonomy
Despite the oxymoron implied by the heading, there is always something new around the corner, and futures change constantly. Moure and Kerr (1950) began dividing *Melipona* ‘subspecies’ into actual species, when they were found to overlap in their
distribution. Lineages, rather than species, were more or less in line with Schwarz’s interpretation, now expressed as a series of related species (Roubik and Camargo 2012). Reproductive isolation, an important concept then as well as now, was implied when two bees shared their range and activity. The *Melipona fasciata* of Schwarz (1932) was properly recognized as a resident of central Mexico (Ayala et al. 2013), not a species with varieties throughout tropical America. They could not appropriately be named variations of a single species.

I might suggest that, for the moment, favorite species (for stingless bees, Meliponini) like *angustula*, *beechei*, *bocadei*, *carbonaria*, *fasciculata*, *laeviceps*, *manaosensis*, *nebulata*, *scutellaris*, *subnitida*, etc., be given without further qualification— but I doubt this idea would be generally followed. The common names, within a single country, often serve the same purpose— but only to the border. A similar notion, however, has led to the current assignment of genera, where subgenera were once entertained, and also to species, where subspecies (geographic variations, primarily in color) were formerly accepted (see Camargo and Pedro 2013).

Schwarz (1948), Michener (1974), Sakagami (1982), Wille (1983) or Sakagami, Inoue and Salmah (1991) accepted only a few genera, like *Meliponula* and *Dactylurina*, *Melipona*, *Hypotrigona*, *Trigona* and *Lestrimelitta*, but also used subgenera. Camargo and Pedro (1992) placed all valid supraspecific taxa at genus level. The subgenus as a concept is criticized or at least used rather infrequently. The valid names are now 32 ‘genera’ in the Neotropics (Camargo 2013), 15 in the Asian and Australian region (Rasmussen 2008) and 9 in the Afrotopics (Eardley and Kwapong 2013; Michener 2013), and a total including all names and fossil (extinct) meliponines (Rasmussen and Cameron 2010) of 61 genera, but with more fossils being discovered, and a few more living genera, that is likely to change. Today, the stingless bees number approximately 56 genera—if all valid names are now taken as genera, rather than subgenera or synonyms. Which will continue to be called these names, and which will cease to be used at generic or subgeneric levels, remains to be seen (Michener 2013). Michener (op. cit.) suggests 26 total valid genera are now living, and uses additional subgenera. The molecular taxonomy available, with several nuclear (slow-changing) genes, so far suggests only a few revisionary moves in which two genera (like *Scaura* and *Schwarzula*, or *Dolichotrigona* and *Trigonisca*) are collapsed into one (Rasmussen and Cameron 2010). One scenario is that all but a few of the stingless bee genera of the day will remain for the Neotropics, a few will be re-instanted for the Afrotopics (Eardley and Kwapong 2013), and several of the other Paleotropical genera will fall. A sustainable meliponine genus, perhaps, is as Padre Moure envisioned it—there are 30 species or less, and they can all be remembered (A. Raw, pers. comm.). And several authors have commented that the meliponines seem to be divided into rather large natural groups, so that is not inconceivable that tribes will again be used, and grouped within a subfamily, or perhaps subtribes will be re-modeled. Moreover, when there is no certainty as to where a species belongs—as is the case for ‘incertae sedis’, it is helpful to have a genus or a categorical group in which to include that species. A genus with only one described species may, later on, include more described species, found with further field work or museum research. For example, the bizarre intraneine cleptoparasite *Trichotrigona extranea* has a second, recently-collected, species (S. R. M. Pedro, pers. comm.). And although genera with one known species, for example *Homostrigona*, *Paratrigonoides*, *Lophotrigona*, or *Meliwillea*, might be merged with sister species or groups, this has little scientific or practical significance.

1.4 Microscopic approaches yield macroscopic results

It seems to me that while stingless bees are the most abundant bees of the tropics, they require a good microscope, material and light source for a definitive identification. It also helps to have them on an entomological pin, with a label. Their species may be similar to each other, but very seldom truly ‘cryptic’ or without visible characteristics that distinguish them. Nonetheless, a complete collection with at least several males and workers, and good judgment, combined with refined molecular or morphometric methods, almost too numerous to list here, should be part of a taxonomist’s tool kit.

The literature, if consulted closely, often provides incentive and guidance for productive research. Wille made it clear that two bees like *Melipona beecheii* are in Costa Rica (Wille 1976). Later we find there are probably a few different species, all currently called *M. beecheii*, in Mexico and Central America (Quezada Euán et al. 2007). Molecular data were of help, but morphological data were always there— awaiting sufficient mass in collection to gain force. This is an exciting and important time to participate in the great reckoning of tropical stingless bees in the
world’s biome, for posterity, prosperity and future decisions. Engel (2011) implies that it is quite an advanced classificatory network, compared to Hymenoptera in general. It is a cooperative process, which relies on much field, laboratory, museum and applied work by people willing a ready to exchange ideas, learn and communicate. Why do they keep changing the names of our stingless bees? Because it really is fun.

References
A little history and guide to taxonomy of Meliponini


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