Distribution and variation among *Melipona favosa favosa* (Hymenoptera: Apidae) in the Caribbean region

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Abstract: The island of Little Tobago appears to be located at the most northerly border of the area of distribution of *Melipona favosa favosa*. Mainland specimens of *Melipona favosa favosa* are larger than, and differ in colouration from insular specimens. In addition there exists considerable variation in colouration between bees from the same nest.

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Introduction

During an expedition with the research vessel "Plancius" in 1987, the first two authors collected several specimens of the stingless bee *Melipona favosa favosa* (Fabricius) (Hymenoptera, Meliponinae) on two Caribbean islands. Even within this one subspecies there appeared to be a striking variation in colouration and size of the specimens. The islands in the Lesser Antilles are of particular interest regarding the distribution of *M. favosa*, because they are on the edge of the northern distribution of the species.

Stingless bees are the most important group of social bees in the tropics, both in numbers as in diversity (Michener, 1974; Wille, 1983; Roubik, 1989). Some 400 species are recognized with the greatest diversity in the Neotropics. Therefore the Neotropics are believed to be the area of origin of stingless bees (Kerr & Maule, 1964).

The occurrence of *Melipona* Illiger on the mainland of South America, as well as north of Panama, raises the question how the dispersal of *Melipona* from South America has taken place. There are two possible routes of dispersal: across the Isthmus of Panama and/or along the islands of a Miocene Caribbean Arc (Camargo et al., 1988). In relation to dispersal theories, the *M. favosa* group is an interesting species group. The mutually exclusive occurrence in very similar regions of Panama and Costa Rica of the closely related species pairs *Melipona compressipes* (Fabricius) (in Panama) – *M. beecheii* Benett (in Costa Rica) and *M. favosa* (Fabricius) (in Panama) – *M. yucatanica* Camargo, Moure & Roubik (in Costa Rica), points to a route along the Caribbean Arc. Were this hypothesis incorrect, it would be very difficult to account for the evolution of species occupying similar regions that were separated until the Pleistocene (Camargo et al., 1988). Clearly more data concerning morphological and ecological differences between species of these four *Melipona* species are needed. In addition, the occurrence on the islands of Dominica, Guadeloupe and Montserrat of *M. variegatipes* Gribodo, a species closely related to *M. favosa* (Schwarz, 1932; Camargo et al., 1988), is evidence for an ancient connection with South America (Camargo et al., 1988).

In the Caribbean region the *M. favosa* group consists of *Melipona favosa* (with its subspecies), *M. yucatanica* and *M. variegatipes*. Schwarz (1932) distinguished seven subspecies of *M. favosa*. *Melipona variegatipes*, by Schwarz considered to be a subspecies of *M. favosa*, was considered to be a good species

by Camargo et al. (1988). Nates Parra & Roubik (1990), revising *M. favosa*, proposed four subspecies, of which two, *M. f. favosa* (Fabricius) (Venezuela, Colombia, Trinidad, French Guiana, Guiana, Surinam) and *M. f. orbignyi* (Guérin) (Brasil, Bolivia, Paraguay, Argentina, Ecuador, Colombia and Panama), occur in the Caribbean region. The subspecies of *M. favosa* have been distinguished on the basis of their distribution, facial maculations, colour of thoracic pile and the extent of metasomal coloured bands (Schwarz, 1932; Nates Parra & Roubik, 1990).

The objectives of this paper are to present our data on the distribution of *Melipona favosa favosa*, to supply information about the morphological variation among specimens of this subspecies (within-nest variation as well as variation between different localities) and to discuss these data with respect to dispersal theories. In addition we will discuss the use of some colour characteristics in distinguishing between subspecies.

For this purpose we compared specimens collected in 1987, with specimens we collected earlier in Trinidad and Surinam, kept in our own collection, and specimens kept in collections of three museums in The Netherlands.

Material and methods

During the "Plancius" expedition in 1987 foraging bees were collected on flowers on the islands of Tobago (11°08'N, 60°50'W-11°20'N, 60°31'W) and Little Tobago (11°18'N, 60°30'W).

The Trinidad specimens were collected from natural nests. Other specimens are kept in our own collection and in the collections of the Zoological Museum, Amsterdam, the National Museum of Natural History, Leiden and the Natural History Museum, Maastricht.

The number of specimens from the different countries and collection sites were: Little Tobago n = 10; Tobago (Fort King George) n = 3; Surinam (Nickerie, Coronie, Coppename river, Boskamp, Paramaribo, Matapika, Commewijne) n = 52; Trinidad (Longdenville, Flannagan Town) n = 38. Of all specimens, body size characteristics and the extent of colour marks on clypeus, metasoma and hind tibiae were measured (table 1). A description was made of the colour of the marks.

For the Trinidad specimens a coefficient of variation (= Standard Deviation*100/mean) was calculated to quantify within-nest variation in size and extent of colour marks. With

Table 1. Descriptive statistics for the bees collected at various localities, and total range of all characteristics. For different localities mean value and one Standard Deviation are given. All measurements given in mm.

		Surinam		Trinidad		Tobago		Little Tobago		total range
s	(n)	(50)		(38)		(3)		(10)		—
i	head l*	2.50	.07	2.38	.84	2.36	.10	2.29	.05	2.20-2.59
z	head w*	3.65	.08	3.41	.14	3.38	.14	3.28	.10	3.12-3.81
e	tib l*	2.71	.14	2.57	.11	2.57	.16	2.43	.06	2.34-3.36
	tib m l	1.71	.33	1.79	.87	1.77	.10	1.59	.09	1.42-2.05
	% tib m*	65.13	3.88	68.89	2.65	68.40	1.48	65.14	3.72	57.4-76.4%
c	clyp m w*	0.32	.08	.022	.06	0.36	.03	0.28	.06	0.15-0.54
o	clyp m l*	0.82	.98	0.66	.11	0.68	.21	0.70	.12	0.44-0.98
l	% clyp m*	32.91	3.89	27.79	4.07	29.07	9.25	30.47	5.03	18.4-39.6%
o	%b1	57.70	6.63	56.19	5.28	65.67	2.08	54.40	6.62	40-74%
u	%b2	16.83	20.70	18.19	12.31	26.33	20.23	7.70	9.36	1-85%
r	%b3	0.14	.59	0.32	.17	0.00	.00	0.10	.32	0-5%
	b3 w*	0.35	.03	0.36	.02	0.39	.00	0.39	.15	0.29-0.39
	% with tib m	32		2.7		0		0		—

head l = length of head (central ocellus-lower rim clypeus); head w = width of head (largest distance including eyes); tib l = length of hind tibia; tib m l = length of colour marking on hind tibia; % tib m = relative size of colour markings on hind tibia; clyp m w = width of colour marking on clypeus; clyp m l = length of colour marking on clypeus; % clyp m = the relative size of the colour marking on the clypeus; %b1, %b2, %b3 = relative length of the interruption in the first, second and third metasomal band; b3 w = width of third metasomal band; % with tib m = percentage of bees having a colour mark on hind tibia. Characteristics given with an asterisk differ significantly between mainland specimens and island specimens (T-test, $p < 0.05$).

this method differences in value of the different characteristics are standardized.

Results

The comparison of specimens of *M. favosa favosa* from the different localities revealed that they differ in various aspects. The biometric measurements are summarized in table 1.

All size parameters of the mainland specimens are significantly larger than those of the insular specimens. In the range from Surinam (on the mainland) towards Little Tobago (at the largest distance from the mainland) the bees become stepwise smaller.

Differences in the extent of the colour marks were as follows: mainland specimens have relatively smaller marks on hind tibiae than insular specimens, relatively larger clypeus marks and a narrower third metasomal band, despite the larger body size.

Regarding to the colours themselves, the colour of the clypeus marks becomes gradually duller from Surinam towards Little Tobago. The marks on the hind tibiae are much duller in specimens from Little Tobago than in specimens from other localities. The colour of the metasomal bands is in Tobago and Little Tobago specimens darker than in specimens from Trinidad and from Surinam. In summary the bees of Little Tobago are the smallest and have the darkest appearance.

There is a considerable variation in some of the morphological characters among nestmates from Trinidad (table 2). In all three nests however, variation in size is relatively small compared to variation in colour pattern.

Table 2. Coefficient of variation (= Standard Deviation *100/mean) within three different colonies from Trinidad. Abbreviations: see table 1.

		colony 1	colony 2	colony 3
s	(n)	(15)	(11)	(12)
i	head l	1.9	2.3	1.7
z	head w	1.6	2.7	2.1
e	tib l	3.3	2.7	2.8
	tib m l	5.2	2.8	5.4
	% tib m	3.3	1.7	5
c	clyp m w	26.7	15.5	20.1
o	clyp m l	12.9	14.6	4.7
l	% clyp m	11.9	14.8	4.5
o	%b1	8	8	10
u	%b2	41.7	37.87	101.8
r	%b3	—	155.8	—
	b3 w	6.8	4.9	5.7

Conclusion and discussion

According to Nates Parra & Roubik (1990) *M. favosa* is a circum-Amazonian bee, having its northernmost population in Panama (9°N). Schwarz (1932) already mentioned the occurrence of *M. f. favosa* on Trinidad (10°05'N)-10°50'N), and our specimens from Little Tobago (11°18'N) were collected even a little further to the North.

In addition to the taxonomic relationship of *M. favosa* and *M. variegatipes* (Schwarz, 1932; Camargo et al., 1988) also the trends in body size and colouration in our specimens of *M. f. favosa*, compared with those characteristics of *M. variegatipes* from Dominica, can possibly be regarded as an argument in favour of an ancient connection between the Caribbean islands and South America. *Melipona variegatipes* can be distinguished from *M. favosa* by the absence of metasomal bands and of colour marks on the clypeus as well as by legs of a much lighter colour, lacking colour marks in var. *lautipes* (Schwarz, 1932), and genital characteristics (Camargo et al. 1988). In appearance *M. variegatipes* is a small, dark coloured *Melipona*, closely related to *M. favosa*. In our specimens there was a trend for bees to become gradually smaller as they originate from populations that are located gradually further away from the mainland. Two specimens of *M. variegatipes* collected on Dominica appeared to be even smaller in size than *M. f. favosa* from Little Tobago (own observations). In addition our island specimens were darker in appearance than our mainland specimens. It is hypothesized that *M. variegatipes* developed from *M. favosa* during the dispersal of the latter across the Caribbean Arc.

Nates Parra & Roubik (1990) used the extent of the interruption in the metasomal bands among the characteristics to distinguish between subspecies of *M. favosa*. They found in *M. f. favosa* an interruption of the first meta-

somal band of ⅓-⅛ and of the second band 0-1/6 as opposed to ½-¼ in the first band and ⅓-<1/6 in the second band in *M. f. phenax* Cockerell. Our finding of 40-74% in the first band and 1-85% in the second band within the subspecies *M. f. favosa*, indicate that this characteristic is not a very useful parameter for distinguishing between subspecies.

Although there is a considerable amount of variation in colouration between bees from the same nest, variation in size among nestmates is low. This generally agrees with results in *Melipona fasciata* Latreille, and is probably related to the communication system used for recruiting nestmates for foraging (Waddington et al., 1986). In *M. favosa* within-nest size variation is somewhat larger than in *M. fasciata*. This could be related to the *M. favosa* colonies being smaller. We hypothesize that a smaller colony has a more unstable larval feeding situation resulting in more variation in worker sizes.

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