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An Adaptive View of Caste Differentiation in the Neotropical Wasp *Polybia* (*Trichothorax*) *sericea* Olivier (Hymenoptera: Vespidae)

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Abstract

The tribe Epiponini comprehends the swarm-founding Neotropical wasps, with several species endemic to Brazil, which are extremely important in studies of social evolution of wasps. The Epiponini diverge in several ways from the definitions of high eusociality, since caste syndromes range from species without morphological caste differentiation to those with complete caste dimorphism, and all species are polygynous. Frequently, indirect studies based on morphometry and physiology are the only solutions to collect data regarding the natural history and caste system in this tribe, since most species are extremely aggressive and build enveloped nests, usually in places of difficult access. We analyzed morphological parameters in seven colonies of the Epiponini species *Polybia* (*Trichothorax*) *sericea* Olivier in different phases of colonial development. Nine body variables were taken and females were classified according to their ovary development and spermathecal contents. The results showed that caste differences in this species are based on a contrast among variables: queens have larger mesosoma and abdomen, but are smaller in head width and wing length. These results suggest that morphological caste differentiation in this species is based mainly on body shape. We considered this combination of characters as being adaptive. We also showed that caste differences varied according to the colony cycle, with more conspicuous differences when queen number is reduced.

Introduction

One of the most important features of social insects is the division of labor among reproductive and non-reproductive females. Since they can be morphologically distinct, understanding caste differentiation is crucial to evaluate the evolutionary trajectories of sociality in these insects (Wilson 1971, Bourke 1999, Oliveira *et al* 2007). In fact, the level of sociality is a function of caste differentiation. Commonly, species with a higher degree of caste asymmetries tend to present a well defined reproductive division of labor, and consequently, a higher degree of sociality (Bourke 1999). Highly eusocial insects, such as honeybees, ants and termites, present conspicuous caste dimorphism and pre-imaginal caste determination.

In this aspect, the Neotropical swarm-founding wasps Epiponini (Carpenter 1997) diverge in several ways from the definition generally given for high eusociality, as in this group, caste syndromes range from species without any morphological caste differences to those with complete caste dimorphism (Richards 1978). Moreover, caste differences may vary according to the colony phase, and this variation may be related to the process of queen selection (Noll & Zucchi 2002). Caste determination is also variable and complex, and may be pre or post-imaginal depending on the species (Mateus *et al* 2004). All Epiponini wasps are polygynous, and queens do not play an important role in the control of social cohesion (Noll & Wenzel 2008). Contrarily to other highly eusocial insects, workers of Epiponini police the reproductive status of queens and eliminate those with lower reproductive potential (West-Eberhard 1973, Nascimento *et al* 2004). This variation in the number of queens may be important to the genetic composition of the colony: when polygyny levels are high, relatedness among queens is low and, consequently, overall relatedness among workers is also low. Such a scenario would act against social cohesion. An opposite situation occurs when levels of polygyny are low and queens are closely related (Hamilton 1972, Queller *et al* 1993, Strassmann *et al* 1998, Nascimento *et al* 2004). Additionally, a recent study showed through gene-based simulations, that cooperative behavior would be favored by multiple matings (Nonacs 2011). This enigmatic scenario involving the Epiponini draws sociobiologists' attention to the real social status of this group (for further discussion see Bourke 1999 and Noll & Wenzel 2008).

Caste differentiation in the Epiponini is a complex trait, since a wide range of different patterns is found (Richards 1978, Noll & Zucchi 2002, Noll *et al* 2004). According to Noll *et al* (2004), four different syndromes are now recognized in the Epiponini: (1) casteless – no morphological differences in size or shape and the presence of females with all ovary developmental conditions (Shima *et al* 1998, Mateus *et al* 2004, Noll *et al* 2004), (2) without a clear morphological distinction, but physiological differences with the presence of intermediate females (Noda *et al* 2003, Noll *et al* 2004, 2010), (3) queens larger than workers, but no shape differences (Noll *et al* 2004), and (4) caste differences based on shape, with queens smaller than workers in some variables and larger in others (Shima *et al* 1994, 1996a,b, 2003, Hunt *et al* 1996, Desuó *et al* 2011).

The Epiponini wasp *Polybia* (*Trichothorax*) *sericea* Olivier is widely distributed throughout South America, especially in Brazil. The nests are usually globose, reddish brown in color, never very large, and commonly built on branches of various trees. Colony size may vary from a few individuals to thousands (Richards 1978). This species belongs to the most diverse genus of Epiponini, which presents several different syndromes of caste differentiation. There are no studies regarding caste differentiation in this species. Therefore, the aims of this study were (1) to investigate the pattern of caste differentiation of *Po*. (*T*.) *sericea* and (2) to explain this pattern within the framework of an adaptive scenario.

Material and Methods

In this study seven colonies of the Epiponini wasp *Po*. (*T*.) *sericea* were analyzed; they were collected in different phases of the colony cycle. Colonies were collected in the following regions: (I) Mirandópolis/SP/Brazil (20º36’58.8”S; 49º27’54”W), (II) Ribeirão Preto/SP/Brazil (21º12’’42’S; 47º48’24’’W), (III) Rio Claro/SP/Brazil (22º24’36’’S; 47º33’36’’W), (IV) Penápolis/SP/Brazil (21º24’59.1”S; 50º04’23”W), (V) Paulo Afonso/BA/Brazil (9º33’13”S;38º29’20”W), and (VI) and (VII) were collected in Senhor do Bonfim/BA/Brazil (10º02’14”S;40º00’43”W). All adult wasps of each colony were immediately killed and fixed in Dietrich’s solution and preserved in ethanol 70%.

A sample of 25% of the adult population of each colony was randomly chosen for morphological studies and had their measurements taken under a binocular stereomicroscope (smallest unit = 0.083 mm). Eight body parts were measured to obtain the morphological data (Fig 1): HW (head width), IDM (minimum inter-orbital distance), MSW (mesoscutum width), AL (alitrunk

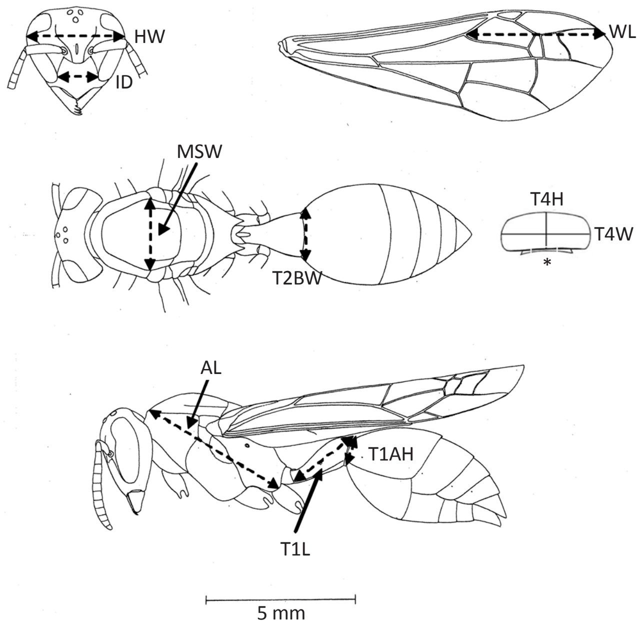

Fig 1 Morphological variables used for morphometric analysis. HW - Head width; IDM - minimum interorbital distance; MSW - mesoscutum width; AL - alitrunk length; T2BW - basal width of gastral tergite 2; T1AH - apical height of gastral tergite 1; T1L - length of gastral tergite 1; T4W – width of tergite 4; T4H – height of tergite 4; WL - partial length of the forewing. *These structures were put against two microscope slices and distended to provide the correct measurement.

length), T1L (length of tergite 1), T1AH (apical height of tergite 1), T2BW (basal width of tergite 2), and WL (wing length). Colonies I, II, III and IV also had the following variables assessed: T4W (width of tergite 4) and T4H (height of tergite 4). Specimens were dissected to check for insemination and ovary development. According to the ovary condition and insemination, females were regarded as workers or queens.

Statistical analyses were performed using SAS 9.2® statistical package and JMP 7.0 linked to the SAS database. The statistical procedures were as follows: (1) the original data were converted into log ranks to facilitate arranging them in a normal distribution; (2) PROC MEANS was used to calculate basic statistics; (3) PROC ANOVA was used to test univariate differences between the arithmetic means of workers and queens of each colony; (4) PROC DISCRIM was used to find a function which maximized the separation between the castes; a classification matrix of each colony was made considering that there was the same prior probability that one individual belonged to one of the two castes; (5) PROC CANDISC was used to perform a canonical analysis of the original data; setting NCAN = 2 provided two axes and produced a canonical scatterplot to visualize the separation of the castes in the different phases of the colony cycle; (6) PROC STEPDISC was used to perform a stepwise discriminant analysis in order to choose the most important variables that discriminate castes in *Po.* (*T.*) *sericea*. We used the option SLENTRY = 0.15, which specifies the significance level for adding variables. In this case, variables with a p-value greater than 0.15 were removed from the model. The procedures (4), (5) and (6) were employed using the original data, in millimeters.

Results

The composition of the colonies is detailed in Table 1. According to the number of immatures and adults, number of meconia, relative age structure and percentage of queens (see Table 1 for further details), colonies were classified I – Pre-emergence; II, III, IV and V – worker production; VI, VII – male production.

Three "types" of ovary development condition were observed in females of *P.* (*T.*) *sericea* : (1) Type A – characterized by filamentous ovarioles without any oocyte development; (2) Type B – ovarioles with slight oocyte development; and (3) Type C – represented by well developed ovarioles with many mature oocytes. Type B was gradually subdivided into B1, B2 and B3 (Fig 2). Queens were associated with type C ovaries and were the only individuals that presented sperm-filled spermathecae. Non-inseminated females with ovary patterns A or B were considered as workers.

The One-Way ANOVA results revealed that queens were overall larger than workers (Table 2). It is worth mentioning that the variables shown in Table 2 were chosen by stepwise discriminant procedure, and thus represent the most important variables to discriminate castes in *P.* (*T.*) *sericea*. From the analysis of the total-sample standardized canonical scores in Table 2, it is evident that

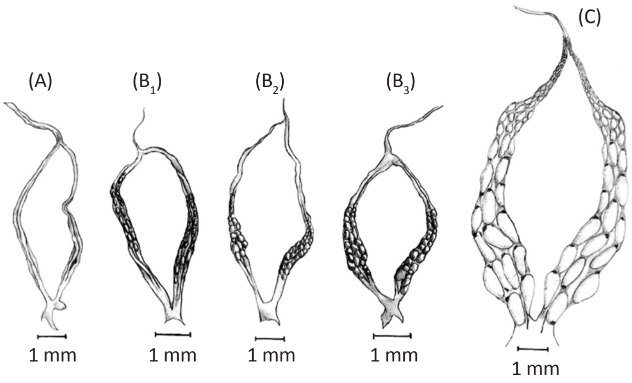

Fig 2 Patterns of ovary development in *Polybia* (*T.*) *sericea*. A – filamentous ovarioles; B – slight oocyte development; C –well developed ovarioles with many mature oocytes. Type B was gradually divided into B1, B2 and B3.

Table 1 Nest composition of the analyzed colonies of *Polybia* (*T.*) *sericea*.

Colonial stage	Nº	Imatures			Meconia	Males	Females			
		Egg	Larva	Pupa			Sampled workers	Queens	Total population	% queens
Pre-emergence	I	-	-	-	-	-	37	63	301	20.9
Worker production	II	+	+	+	1	-	67	46	676	6.8
	III	+	+	+	1	-	50	13	653	2.0
	VI	+	+	+	1	-	50	21	411	5.11
	V	+	+	+	1	-	80	8	92	8.7
Male production	VI	+	+	+	2	38	150	21	621	12.3[1]
	VII	+	-	+	2	2	126	7	454	5.26[1]

[1] Estimated queen´s percentage. The % of queens was calculated based on the sample size.

Table 2 Statistical analysis of morphometric data for *Polybia* (*T.*) *sericea* queens and workers. The variables shown are those considered as the most important based on stepwise discriminant analysis.

Colonies	Variables[1]	ANOVA (mean ± sd)			Discriminant analysis			Canonical coefficients[2]
		Queens	Workers	F	Wilks' Lambda	F to Enter	P > F	Can1
I	T1L	3.270.12	3.16 ± 0.14	15.19[3]	0.86	15.19	< 0.001	0.87
	WL	5.83 ± 0.15	5.73 ± 0.16	10.04[3]	0.84	2.93	< 0.001	0.90
	T4H	1.86 ± 0.25	1.88 ± 0.08	0.14[ns]	0.80	4.60	< 0.001	-0.55
II	T4W	5.43 ± 0.23	4.90 ± 0.17	134.98[3]	0.39	134.98	< 0.001	1.18
	WL	5.83 ± 0.14	5.92 ± 0.17	5.68[4]	0.33	14.93	< 0.001	-0.83
	MSW	2.52 ± 0.06	2.44 ± 0.07	23.09[3]	0.30	11.66	0.001	0.61
	T1L	3.40 ± 0.11	3.29 ± 0.12	16.22[3]	0.27	7.91	< 0.01	0.41
	T1AH	1.00 ± 0.07	0.88 ± 0.07	45.97[3]	0.26	3.44	0.07	0.33
	HW	3.55 ± 0.10	3.54 ± 0.07	0.11[ns]	0.25	3.70	0.06	-0.32
III	T1L	3.50 ± 0.06	3.06 ± 0.13	126.76[3]	0.32	126.76	< 0.001	1.25
	T4W	5.65 ± 0.12	5.14 ± 0.19	78.68[3]	0.29	6.12	< 0.05	0.48
	WL	6.04 ± 0.16	5.56 ± 0.24	44.52[3]	0.28	3.56	0.06	-1.17
	HW	3.68 ± 0.09	3.40 ± 0.08	108.52[3]	0.24	7.74	< 0.01	1.12
IV	HW	3.36 ± 0.09	3.48 ± 0.11	16.58[3]	0.81	16.58	< 0.001	-1.63
	T1L	3.32 ± 0.15	3.30 ± 0.33	2.07[ns]	0.60	23.95	< 0.001	0.64
	T4H	1.99 ± 0.06	1.94 ± 0.06	9.01[4]	0.50	12.70	< 0.001	0.35
	MSW	2.39 ± 0.10	2.38 ± 0.11	0.24[ns]	0.43	10.21	< 0.01	0.67
	T4W	5.42 ± 0.11	5.32 ± 0.16	8.05[4]	0.40	4.18	< 0.05	0.42
CIII	T2BW	1.55 ± 0.04	1.45 ± 0.05	21.12[3]	0.80	21.12	< 0.001	0.77
	HW	3.50 ± 0.08	3.54 ± 0.06	3.11[ns]	0.75	5.52	0.0211	-0.57
CIV	T2BW	1.60 ± 0.05	1.49 ± 0.05	85.64[3]	0.66	85.64	< 0.001	1.00
	HW	3.56 ± 0.06	3.62 ± 0.04	27.49[3]	0.53	41.00	< 0.001	-0.63
	WL	5.77 ± 0.22	5.95 ± 0.13	29.41[3]	0.49	13.33	< 0.001	-0.44
	IDm	1.67 ± 0.05	1.65 ± 0.04	2.71[ns]	0.48	4.93	0.027	0.25
	T1L	3.59 ± 0.08	3.54 ± 0.07	8.37[3]	0.47	3.50	0.063	0.21
CII	T2BW	1.63 ± 0.05	1.53 ± 0.06	14.90[3]	0.90	14.90	< 0.001	0.41
	WL	5.85 ± 0.05	6.01 ± 0.15	7.61[4]	0.84	8.81	0.0036	-0.50
	MSW	2.50 ± 0.04	2.40 ± 0.09	7.42[4]	0.82	3.76	0.0547	0.40
	T1L	3.65 ± 0.05	3.52 ± 0.12	7.40[4]	0.80	2.34	0.128	0.41
	HW	3.54 ± 0.07	3.58 ± 0.06	2.11[ns]	0.78	3.56	0.061	-0.66

[1] Most important variables after Stepwise Discriminant Procedure in SAS software [For more details on the chosen variables see Material and Methods sections (Fig 1)]; [2] Total-Sample Standardized canonical coefficients; [3] ANOVA $P < 0.001$; [4] ANOVA $P < 0.01$; [ns] ANOVA non significant.

CAN1 is defined by a contrast between head and wing size versus abdominal variables. Queens are characterized as larger individuals (especially in the abdominal variables), with smaller head width and wing length. In colony V, for example, the canonical score was 0.77 for T2BW and -0.57 for HW. This contrast means that for both variables chosen using a stepwise discriminant function, caste differences in this phase were represented mostly by queens with larger T2BW and smaller HW. This assumption holds for most of the colonies (Table 2), except for colony III, in which the canonical score was positive for HW.

Canonical scatterplots (Fig 3) indicated that castes can be separated into queens and workers; however, such separation was less evident in colony I and more

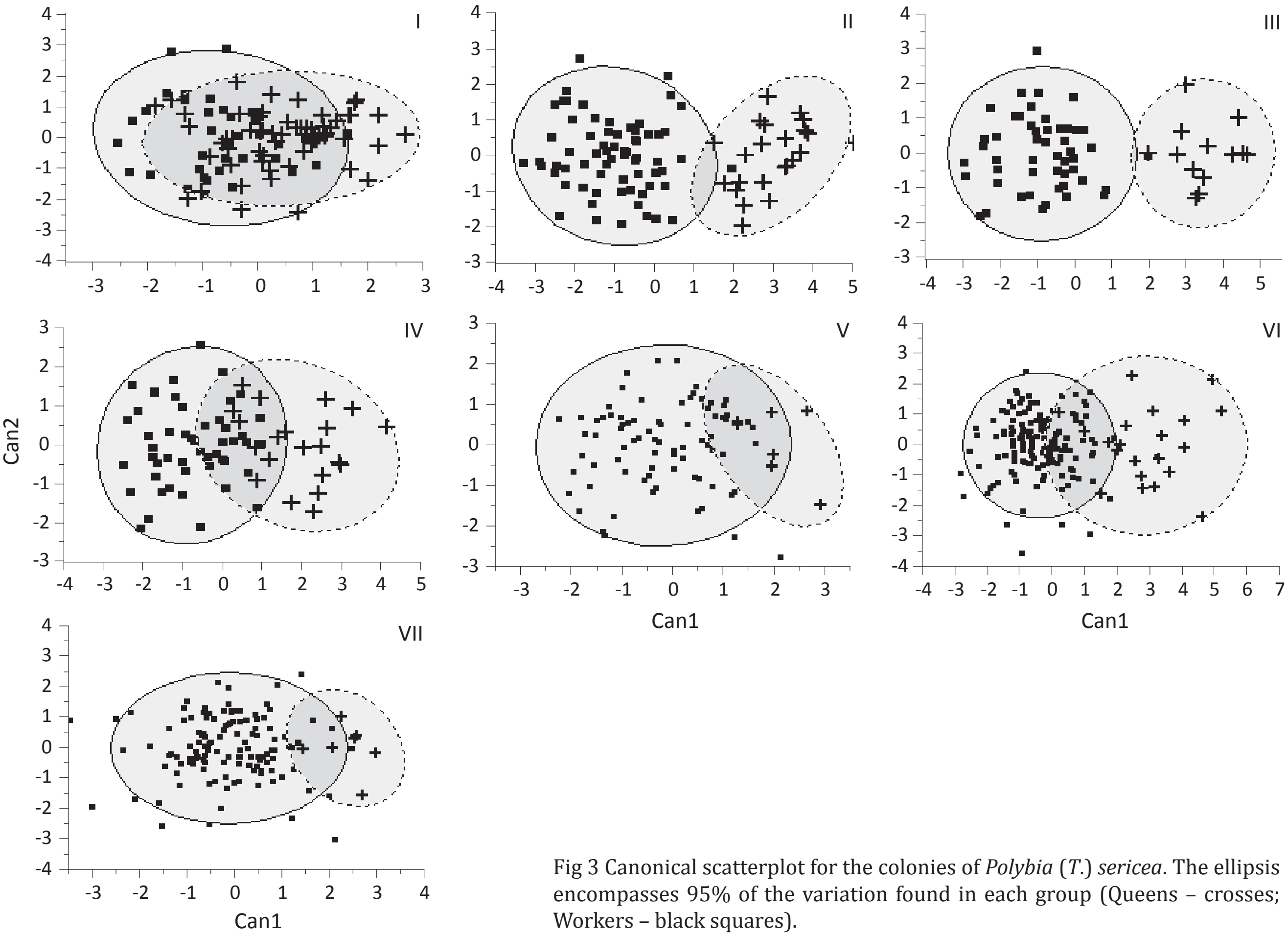

Fig 3 Canonical scatterplot for the colonies of *Polybia* (*T.*) *sericea*. The ellipsis encompasses 95% of the variation found in each group (Queens – crosses; Workers – black squares).

conspicuous in colony III (see the overlapping area of Fig 3). Queens have higher values in CAN1 than workers (Fig 3), and linking this information with the canonical scores (Table 2), it is possible to define the morphological differences between queens and workers in each colony phase.

The values of Wilk´s lambda (Table 2) ranged from 0.4 to 0.8, which indicates, according to Noll *et al* (2004), that the power of discrimination of the variables ranged from moderate to low. Finally, the classification matrix obtained after discriminant function analysis (Table 3) showed that queens were only 100% correctly classified in colonies II and III, indicating that queens from these colonies were more distinct morphologically from workers, resulting in a higher degree of caste differentiation than in the other colonies.

Discussion

The genus *Polybia* (Lepeletier) is the most diversified group within the Epiponini. Caste differentiation in this taxon is complex and several syndromes are found (Noll *et al* 2004, Noll & Wenzel 2008). Our data showed that castes of *Po*. (*T.*) *sericea* differed morphologically, however such morphological differences, given by size, were less conspicuous than in other Epiponini genera (*Agelaia* and *Apoica*) and species from *Polybia*, *Polybia lilliacea* (F.) and *Polybia* (*Trichothorax*) *ignobilis* (Haliday). Nevertheless, queens of *Po*. (*T.*) *sericea* were larger than workers in some of the body variables, yet smaller in others, and similar patterns were also found in other lineages of the Epiponini (Noll *et al* 2004, Noll & Wenzel 2008), but queens were considerable larger than workers (Wilk´s Lambda ranged from 0.1 to 0.5) (Desuó *et al* 2011). Based on morphological data sets, Jeanne *et al* (1995) hypothesized that such pattern of caste differences is related to a differential growth of imaginal discs during the immature period, which results in differences in adult shape, rather than size. However, there are no studies regarding the development of imaginal discs in the Epiponini (Desuó *et al* 2009, 2011).

Queens with larger T2BW is the ancestral condition of the Epiponini, and also a widespread pattern in this tribe (Noll & Wenzel 2008). In social insects, larger abdomen may be considered a predictable trait for queens, as they are frequently physogastric. However, if queens have

Table 3 Classification matrix after discriminant function analysis.

Colony		% Correct classification	Predicted classification	
			Workers	Queens
I	Workers	56.75	21	16
	Queens	84.12	10	53
	Total	80.45	40	60
II	Workers	98.51	66	1
	Queens	100.00	0	23
	Total	99.22	67	23
III	Workers	98.00	49	1
	Queens	100.00	0	13
	Total	100.00	50	13
IV	Workers	90.00	49	1
	Queens	85.71	3	18
	Total	87.85	48	23
V	Workers	98.75	79	1
	Queens	37.50	5	3
	Total	93.18	84	4
IV	Workers	98.67	148	2
	Queens	80.95	4	17
	Total	96.49	152	19
VII	Workers	99.21	125	1
	Queens	57.14	3	4
	Total	96.99	128	5

larger ovaries and are specialized in laying eggs, then they should present adaptations in their external morphology to support their ovary status. These adaptations, such as distended tergites, should appear primarily in the abdominal region allowing the abdominal cavity to carry a larger ovary. Considering that insects do not grow during adult life, these structural modifications may represent differences in developmental routes in the pre-imaginal stages of queens and workers. These different developmental paths could lead to higher growth of abdominal structures in queens, and then could represent the first step into the development of specialized castes in the Epiponini.

Queens with smaller head width and wing length is a common pattern of caste differences in the Epiponini (Noll & Wenzel 2008). Such variation from the ancestral condition ("egglayer equal to non-egglayer", see Noll & Wenzel 2008) may represent an adaptation to a higher caste specialization. Queens with smaller head width are reported in species with substantial caste differences (Noll *et al* 2004, Noll & Wenzel 2008). In general, queens spend more time in the colony performing reproductive tasks (egg-laying), whereas workers are mostly responsible for foraging activities (O´Donnell 1991). Foraging involves the ability of interacting with the environment and a better capacity to fly (Lima & Prezoto 2003, Gomes *et al* 2007). These requirements may change the physiological status of individuals and thus workers may have larger brains and wings. Jones *et al* (2009) showed that the volume of the mushroom bodies of workers of *P. aequatorialis* (Zavattari) increases as they progress from in-nest activities to forage. It is noteworthy that the canonical score of HW was positive in colony III, indicating that queens were also larger than workers in this body variable.

Our data also showed that the morphological caste differences of *P.* (*T.*) *sericea* varied according to the colony cycle, and that the differences between queens and workers were apparently larger when the number of queens was low (Table 1, Fig 3-III), a trend already shown by others (Noll & Zucchi 2000, 2002, Pizarro *et al* 2009, Desuó *et al* 2011). Therefore, variations in the number of queens and the observed caste differences appear to be related, leading to the conclusion that selection favors larger and more productive queens (queens with higher quantities of fat body and more developed ovaries).

The variance in the number of queens is also an important reproductive trait of the Epiponini, as it affects the genetic relatedness of nestmates within the colony. Usually colonies with a few or a single queen favor the production of new queens while colonies of multiple queens favor the production of males. This occurs because workers are three times more closely related to their sisters than to their brothers in single-queen colonies and equally related to their nieces and nephews in multiple-queen colonies (Strassmann *et al* 1998). In most social insects the production of daughter colonies are tied to the production of new queens. In the Epiponini, however, there is a disconnection between these two events which allows the Epipoini to form new colonies during the most favorable season, contributing to ecological success of this tribe in the neotropical region (Strassmann *et al* 1998).

The literature regarding caste in the Epiponini establishes two main strategies for caste determination: (1) pre-imaginal, in which queens form morphological clusters distinct from workers and (2) post-imaginal caste differentiation where castes are more flexible and non-reproductive resemble reproductive adults (Noll *et al* 2010). Our data clearly indicate that caste determination in *P.* (*T.*) *sericea* is pre-imaginal. The strategy adopted by the studied species, as well by other Epiponini, ensures that workers may have a lower chance to achieve a reproductive status than in species in which caste differences are only slight or absent. In fact, Noll *et al* (2010) proved that in species with slight caste differentiation, such as *Leipomeles dorsata* (Fabricius), workers may become reproductively active.

Finally, the pattern of caste differentiation showed in this study seems to operate in other lineages of Epiponini as well, such as *Agelaia*, *Apoica* and other *Polybia* (Pizzarro *et al* 2009). Some of these lineages are not close phylogenetically to *P*. (*T.*) *sericea*, which corroborates the view that caste evolution in the Epiponini is complex and that the different syndromes of caste differentiation found in this tribe probably evolved several times in the different lineages. (Noll *et al* 2004, Noll & Wenzel 2008).

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