CASTE DIFFERENCES AND RELATED BIONOMIC ASPECTS OF *CHARTERGELLUS COMMUNIS,* A NEOTROPICAL SWARM-FOUNDING POLISTINE WASP (HYMENOPTERA: VESPIDAE: POLISTINAE: EPIPONINI)

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Abstract.—Five colonies of *Chartergellus communis,* a Neotropical swarm-founding social wasp, were analyzed in order to determine morphological differences between queens and workers. Although castes could be differentiated by color patterns, morphological differences were practically absent in three out of the five colonies. In the two other colonies, we found queens smaller than workers in all the five measured characters in one colony while in the other queens were larger than workers in the same five characters. The importance of such caste variation according to colony is discussed. Colonies contained a large variety of individuals with different kinds of ovarian development, including intermediates between queens and workers. The occurrence of such intermediate females and their role in different wasp taxa is discussed.

Key words: Polistinae, Epiponini, *Chartergellus communis,* caste differences, colonial cycle, wasp productivity.

Social organization in the Epiponini (Carpenter, 1993) is poorly known, which certainly reflects the complex bionomic characteristics of this Neotropical tribe of social wasps. Von Ihering (1903, 1904) and Ducke (1910) documented the polygynous organization of their societies and reproduction by swarming. West-Eberhard (1973, 1978), however, showed that polygyny is not universal because *Metapolybia aztecoides* alternates from polygyny to oligogyny and, eventually, monogyny in the course of its colony cycle. Such a cycle may explain monogynic records in other epiponine wasp species (Richards, 1978; West-Eberhard, 1973). This cyclical oligogyny (West-Eberhard, 1978) seems to be important in the maintenance of high genetic relatedness found in the Epiponini (Queller et al., 1988, 1993; Hughes et al., 1993).

Recent studies on *Parachartergus colobopterus* (Strassmann et al., 1998) demonstrated that the production of new queens occurs when colonies are 9–12 months old. In this species, however, the production of new swarms is concentrated in the rainy season (Strassmann et al., 1997), which clearly shows that this event is dependent on ecological factors. Nonetheless, the tropical environment in which the Epiponini thrive has rendered colony-cycles much more plastic (asynchronous) than those in the temperate climates (synchronous). The onset of nest foundation, for instance, which is limited to the beginning of the favorable season in the temperate zone species, shows a wide distributional pattern in the Neotropics spanning several months and seasons, excepting only the harshest part of the winter-dry period. Asyn-

chronous nest founding has been demonstrated in *Protopolybia acutiscutis* (Naumann, 1970), *Protopolybia exigua exigua* (Simões et al., 1996) and *Polybia paulista* (Simões and Mechi, 1983).

Another important aspect of epiponine biology is the frequent presence of ovary-developed but uninseminated females in the colonies of several species (Richards and Richards, 1951). These individuals were called intermediates, and Richards (1971) assumed that their role is the production of either trophic eggs or males.

In epiponines, queens generally tend to be larger than workers as in *Protonectarina silveirae* (Shima et al., 1996b), but the most conspicuous size and color differences among epiponine wasps have been found in some *Agelaia* spp. such as *A. flavipennis* (Evans and West-Eberhard, 1970), *A. areata* (Jeanne and Fagen, 1974), and *A. vicina* (Sakagami et al., 1996; Baio et al., 1998). In *Pseudopolybia vespiceps,* caste differences are slight and intermediates are present (Shima et al., 1998). In *Parachartegus fraternus,* differences are very slight or undetectable externally, and so queens are not obviously different from workers and intermediates (Richards, 1978). However, in some groups, queens are significantly smaller than workers in some characters and larger in others (Richards 1971, 1978; Shima et al., 1994). According to Jeanne et al. (1995), who studied *Apoica pallens,* this is explained by non-size-based differences in allometry attributed to reprogramming of larval growth parameters in queens versus workers (Wheeler, 1991; see also O'Donnell, 1998). Such a pattern is apparently quite common in Epiponini wasps, as it was detected also in *Epipona guerini* (Hunt et al., 1996), *Pseudopolybia difficilis* (Jeanne, 1996), *Apoica flavissima* (Shima et al., 1994), *Polybia dimidiata* (Shima et al., 1996a) and *Agelaia vicina* (Baio et al., 1998). The purpose of the present paper is to analyze the colony composition and caste differences of *Chartergellus communis.*

MATERIAL AND METHODS

Five colonies of *Chartergellus communis* were collected by spraying ether on the nest very early in the morning. Preferences were given to colonies at certain developmental stages defined as (1) pre-emergence of workers, (2) emergence of workers and (3) male producing, and at different months: Colony I (02/02/1995), colony II (03/11/1995) and colony III (20/01/1996) were collected in Pedregulho, São Paulo State, SE Brazil (20°09′S–047°37′W); colony IV (01/04/96) and colony V (02/04/96) were collected in Nova Xavantina, Mato Grosso State, CW Brazil (14°32′S–052°26′W). The adults were put in Dietrich's fixative for 72 h and thereafter kept in 70% ethanol. The combs were separated and the number of cells and the presence of immatures were counted. Productivity was estimated by counting of meconial wastes found in some cells.

In order to detect caste differences the following five external body parts were manually measured in each female: head width (HW), alitrunk length (AL), width of mesoscutum (MSW), basal width of tergum II (T2BW) and partial length of forewing (WL) (see Fig. 1 in Shima et al., 1994 for more details). One hundred individuals were chosen randomly (except for colony II of which the whole population was measured): Later, all queens were found and measured. In that way, we measured 142 individuals in colony I, 20 individuals in colony II, 101 individuals in colony III, 100 individuals in Colony IV and 102 individuals in colony V. In

addition, color patterns and other morphological characteristics were examined in 25 queens, 50 workers and 3 intermediates.

We examined ovarian condition by dissecting all individuals under a stereomicroscope. In order to analyze insemination, the spermatheca was removed and put on a slide in a 1:1 solution of glycerin and alcohol (70%). The presence of sperm cells was detected by using a microscope.

Statistical analyses were performed using SAS Program Package for PC computers. Queen-worker difference for each variable was tested by Bonferroni *t*-tests after One-way Anova analyses. Stepwise discriminant analysis was used to identify the most significant contributors to caste difference. Later, the most discriminant character was used as the independent variable for size-adjusted caste contrasts, dividing the other variables to yield the relative variables. Analysis of covariance was used to test for homogeneity of slopes in queen vs. worker contrasts for those variables found to differ significantly by the stepwise discriminant analysis. Squared Mahalanobis distances (D^2) were used as an indicator of changes between casts in the different colonies analyzed. Two measured characters, which could better discriminate among different females in most of the analyzed colonies, were selected and employed in Fig. 3 for caste discrimination.

RESULTS

Nest site—According to Richards (1978), *Chartergellus communis* inhabits preferentially areas of cerrado and cerradão. The nests collected for this study were found in the following localities: Nests I, II and III were in open areas close to pasture fields and cerradão, nest IV in a urbanized area close to cerrado, and nest V in an orchard. This species shows plasticity of nest substratum. Nest I was collected in a trunk of *Eucalyptus* sp. 2.20 m high; nest II was fastened in a trunk of *Acrocomia aculeata,* 4 m high; nest III was located in the door of a wood hut, 2 m high; nest IV located in a branch of *Mangifera indica,* 2.50 m high, and nest V was fastened in an elevated water tank, 3.40 m high. In the municipal district of Pedregulho, São Paulo State SP., nests (N = 3) of *C. communis* were observed built on storerooms and directly on rocks in a ravine and in Bonito, Mato Grosso do Sul State, on a wooden post fence (N = 2), (S. Mateus, pers. obs.).

Nest architecture, colony composition and colony phase. The envelope is of predominantly gray coloration and is made with long vegetable fibers. The construction lines are parallel, giving a grooved aspect to the surface. In the upper part of the envelope (Fig. 1A), an area composed of thicker vegetable fibers strongly stuck to each other and to the substratum with salivary substance gives to that area a spongy aspect (five paper pillars or floss between substrate and envelope margin, particularly on the inside of the upper region, as described by Wenzel, 1998). The entrance of the nest is located in the lower part of the envelope (Fig. 1C), and measured 1 cm in diameter on the average, with a border in a ring form measuring 4 mm height on the average. The internal part of the envelope is entirely impregnated with glossy material of glandular origin. The envelope is very well camouflaged, giving great protection against the attack of some predators. The coloration of the envelope is always very similar to the substratum. Accompanying the grooves there are non-fibrous vegetable materials in a variety of colors such as vegetable coal (black) and
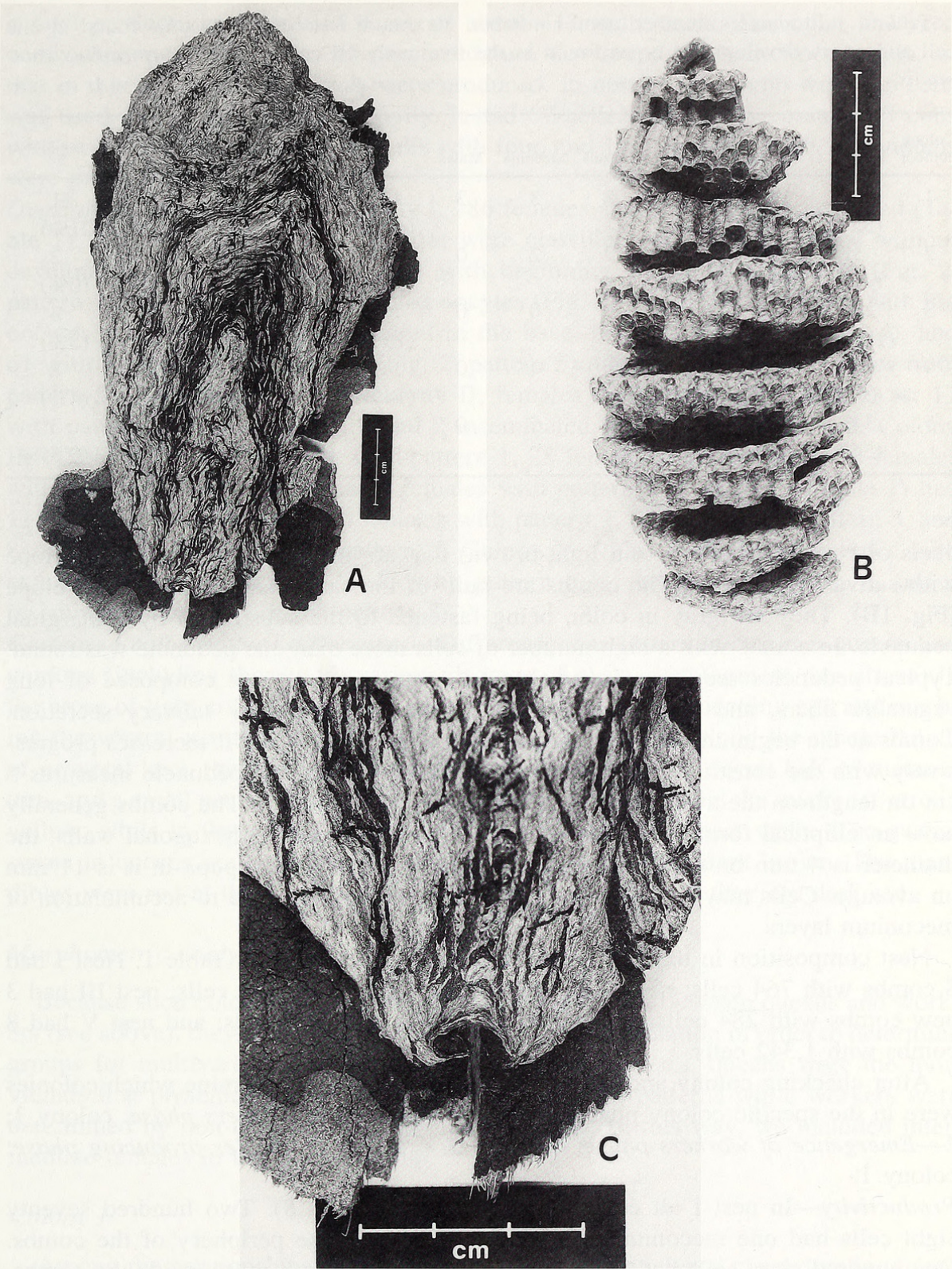
Fig. 1.   Nest of *Chartergellus communis*. A—Envelope; B—Combs and C—Nest entrance.

Table 1. Immatures number, combs number, maximum number of meconia found in one cell and ovary development types found in the five analyzed colonies of *Chartergellus communis*.

Colony number	Eggs	Larvae	Pupae	Combs	Meconia	Males	Ovary development types 1	2	3	4	5
1	161 (32%)	147 (29%)	196 (39%)	8	3	3	139 (49%)	70 (24%)	14 (5%)	2 (1%)	61 (21%)
2	52 (43%)	52 (43%)	17 (14%)	2	2	0	17 (85%)	1 (5%)	0	0	2 (10%)
3	281 (100%)	0	0	3	0	0	170 (78%)	28 (13%)	12 (6%)	0	8 (3%)
4	168 (33%)	121 (24%)	221 (43%)	6	4	0	115 (54%)	80 (38%)	9 (4%)	0	8 (4%)
5	343 (56%)	207 (34%)	61 (10%)	8	5	0	192 (32%)	356 (60%)	41 (7%)	1 (0.2%)	3 (0.8%)

peels of bark (dark-brown and light-brown) that are incorporated into the envelope with salivary substance. The combs are built of the same material as the envelope (Fig. 1B). They are gray in color, being fastened to the substratum by a marginal peduncle. In combs with a high number of cells more than one peduncle was found. Typical peduncles are 2 cm in height and 1 cm in width, are composed of long vegetable fibers, and are strongly stuck to the substratum by salivary secretion. Combs at the beginning of construction have a small base, and it increases progressively with the construction of new cells. In older combs the peduncle measures 5 cm on length on the average for 4 cm height and 2 cm width. The combs generally have an elliptical form. Cells face down, with simple parallel hexagonal walls; the diameter is 4 mm on average, and the height of a cell with a pupa in it is 11 mm on average. Cells may be lengthened after adult emergence due to accumulation of meconium layers.

Nest composition in the five analyzed colonies is detailed in Table 1. Nest I had 8 combs with 764 cells; nest II had two small combs with 124 cells; nest III had 3 new combs with 284 cells; nest IV had 6 combs with 761 cells; and nest V had 8 combs with 1,342 cells.

After checking colony and nest composition, we could determine which colonies were in the specific colony phases: 1—*Pre-emergence of workers phase*: colony 3; 2—*Emergence of workers phase*: colonies 2, 4 and 5; 3—*Males producing phase*: colony 1.

Productivity—In nest I all combs were examined (N = 8). Two hundred seventy eight cells had one meconium; these were located in the periphery of the combs. One hundred sixty cells had two meconia and were located more inside the combs, and in 44 cells located close to the peduncle three meconia were found. These results suggest that about 730 individuals were produced. In nest II there were 43 cells with one meconium and 9 cells with two, thus, 61 individuals were produced. Nest III was of recent foundation and no meconium was found. In nest IV productivity was evaluated in two combs. The largest had 180 cells; of these, 30 contained one meconium, 82 had two meconia, 50 had three meconia and 17 cells had 4 meconia; for

a total productivity from this comb of about 412 individuals. The other analyzed comb contained 76 cells; in 35 one meconium was found; 28 had two meconia, so that in this comb 91 individuals were produced. In nest V, one comb with 256 cells was used to evaluate the productivity. It had 67 cells with one meconium, 57 cells with two, 63 cells with three, 53 cells with four, and 16 cells with 5 (662 individuals were produced in this comb).

Ovarian development—From colony I, 286 females and 3 males were collected (Table 1). After ovary dissection females were classified as: 139 with ovary without development (Fig. 2, pattern 1), 70 with beginning of oocyte formation (Fig. 2, pattern 2), 14 with small well defined oocytes (Fig. 2, pattern 3), 2 females with big oocytes ready for oviposition located in the base of ovary (Fig. 2, pattern 4), and 61 with well-developed oocytes (Fig. 2, pattern 5). Only 54 out of 61 females from pattern 5 were inseminated. In colony II, females were classified (Table 1) as: 17 with pattern 1, 1 with pattern 2 and 2 inseminated females with pattern 5. Colony III (Table 1) had 170 females with pattern 1, 28 females with pattern 2, 12 females with pattern 3, and 8 inseminated females with pattern 5. Colony IV (Table 1) had 115 females with pattern 1, 80 females with pattern 2, 9 females with pattern 3, and 8 inseminated females with pattern 5. Colony V (Table 1) had 192 females with pattern 1, 356 with pattern 2, 41 with pattern 3, 1 female had pattern 4, and 3 inseminated females had the pattern 5.

Caste and color pattern differences—Difference was observed between queens and workers (including those with various degrees of ovary development, see above) in the areas of light coloration: in the gena with a wide streak, touching eye and reaching the ventral margins from top of eye to near mandibles, along the whole length of pronotal keel, the hind margin of pronotum narrowly, the dorsal half of metanotum, and a small posterior corner of mesoscutum. In the workers the marks are strong yellow, while in the queens these marks are light yellow to near white. The gastral sterna in queens are light brown, while in workers they are dark brown. The mandibles were red at the basal half in queens, while in workers they are dark red.

Morphometric analyses

Because such color attributes were efficient to separate between queens and workers (see above), they were used in association with insemination in order to determine groups for multivariate analyses. In the following analyses, queens were the individuals that presented insemination and specific color patterns while workers were determined by non-insemination and color patterns. In this way, we included intermediate females in the worker group.

Colony I

Among the relationships of the averages of the five analyzed characters in queens and workers (Table 2), statistically significant differences between castes were found in all analyzed characters. The significance test (t-test, $P < 0.05$) showed that queens are slightly smaller than workers in colony I of *C. communis* (Fig. 3.1).

The results of the stepwise discriminant analysis based on the nine characters also showed that the most contributing characters were: HW, MSW and T_2BW. The great contribution to total variance was due to MSW. In accordance with multivariate
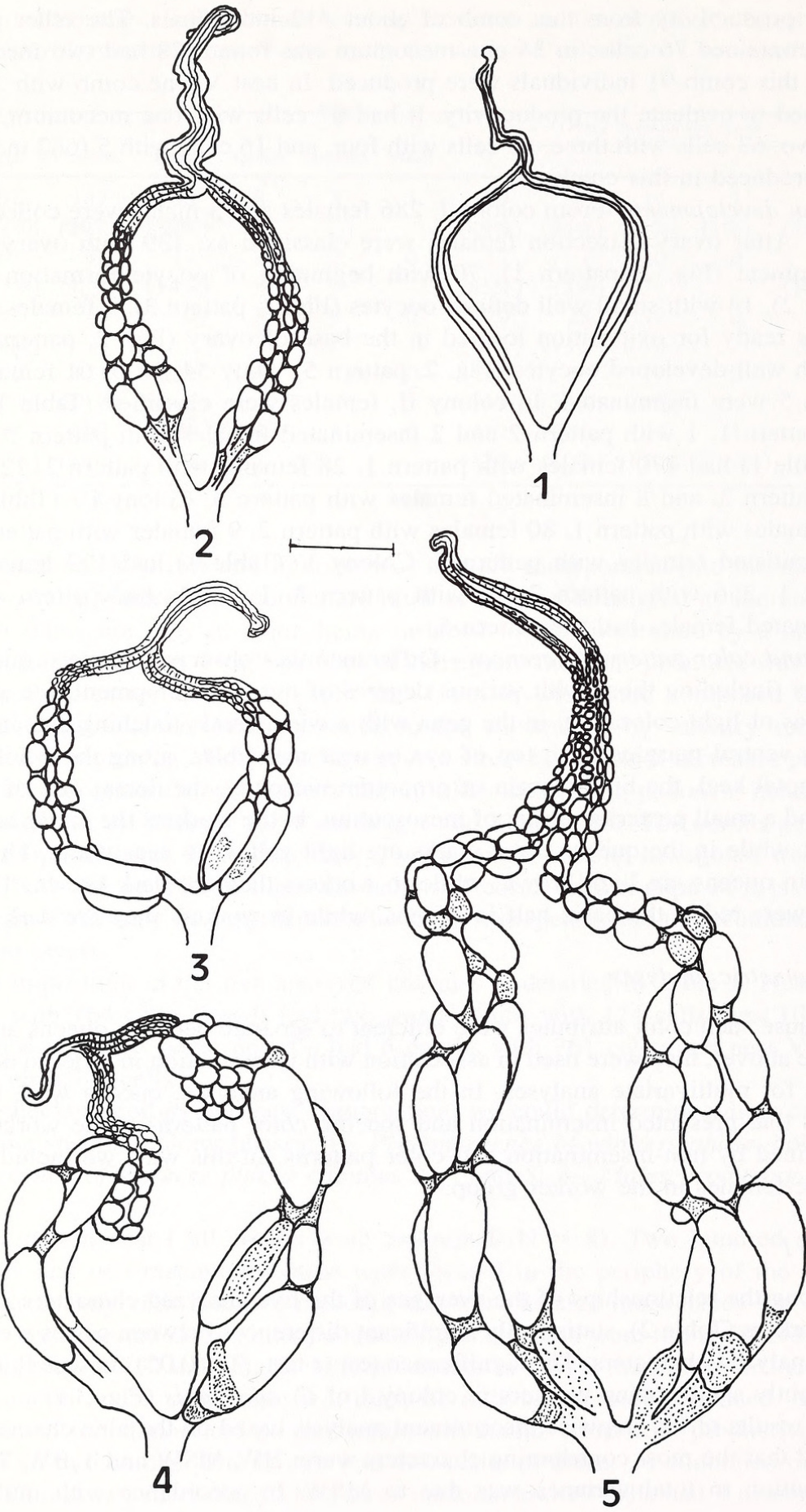
analyses of other social wasps (Jeanne et al., 1995; Jeanne, 1996; Hunt et al., 1996) we used MSW as an independent variable for size-adjusted contrasts because it appeared as one of the greatest factors contributing to total variance between castes in the three analyzed species (see above). Each of the four other characters was divided by MSW to yield four new, relative variables. The following greatest factors were found after stepwise discriminant analyses: HW, AL and T_2BW (Table 2). These variables were independently analyzed using covariance analyses. Queens and workers significantly differ in slope only in T_2BW (F = 1395.2, $P < = 0.0001$).

Generalized Mahalanobis distance (D^2: Anderson, 1968) was statistically significant (D^2 = 2.65; F = 16.32, $P < 0.0001$) indicating slight but significant differences between the castes. In fact, comparisons between predicted and observed classifications showed that workers were 88.37% correctly classified by the method and queens were 66.07% correctly classified.

Colony II

Among the relationships of the averages of the five analyzed characters in queens and workers (Table 3), statistically significant differences between queens and workers were found in all analyzed characters. The test (*t*-test, $P < 0.05$) showed that queens are larger than workers in all five analyzed characters in the colony II of *C. communis* (Fig. 3.2).

Results of the stepwise discriminant analysis based on the five characters also showed that the greatest factors were: MSW, AL and WL. The largest contribution to total variance was due to WL. Using WL as an independent variable for size-adjusted contrasts isolated AL after stepwise discriminant analyses (Table 3). These variables were independently analyzed using covariance analyses. Queens and workers differed significantly in slope in MSW (F = 13.08, $P = 0.02$), AL (F = 8.74, $P = 0.009$) and T^2BW (F = 11.59, $P = 0.003$).

Generalized Mahalanobis distance (D^2: Anderson, 1968) was statistically significant (D^2 = 49.67; F = 9.68, $P = 0.0004$) indicating significant differences between the castes. In fact, comparisons between predicted and observed classifications showed that workers were 100% correctly classified by the method and queens were 100% correctly classified.

Colony III

There were no statistically significant differences between queens and workers in any analyzed character (*t*-test, $P < 0.05$) (Table 4), in colony III of *C. communis* (Fig. 3.3).

Results of the stepwise discriminant analysis based on the five characters also showed no difference between the castes. Using the forward procedure for stepwise

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Fig. 2. Grades of ovarian development in *Chartergellus communis*. 1—ovaries without development, 2—ovaries with beginning of oocyte formation, 3—ovaries with small well defined oocytes, 4—ovaries with big oocytes ready for oviposition located in the base of the ovary; 5—ovaries with well-developed oocytes.

Table 2.   Morphometric caste differences in *Chartergellus communis* (Colony I).

| Characters | Means ± SD | | *t*-test | Stepwise discriminant analyses | | T_2BW as the independent variable | |
	Queens (N = 56)	Workers (N = 86)		Contributor variables	F	Contributor variables	F
HW	3.607 ± 0.075	3.663 ± 0.073	4.4*	X	4.30***	X	9.50**
MSW	2.980 ± 0.086	3.055 ± 0.099	4.6*	X	23.07*	X	3.00#
AL	4.943 ± 0.191	5.166 ± 0.180	7.0*				
T_2BW	3.128 ± 0.083	3.209 ± 0.092	5.3*	X	4.42***	X	2.61#
WL	4.324 ± 0.133	4.428 ± 0.117	4.9*				

*$P < 0.001$, **$P < 0.02$, ***$P < 0.05$, # not significant ($P > 0.05$).

discriminant analysis for castes as the group variable, any variable was included in the model, indicating that any character employed would explain the variation equally well.

Colony IV

Among the relationships of the averages of the five analyzed characters in queens and workers (Table 5), only wing length (WL) was statistically smaller in queens in colony IV of *C. communis* (Fig. 3.4).

Results of the stepwise discriminant analysis based on the five characters also showed that the greatest factors were: MSW, AL and WL. The great contribution to total variance was due to WL. Using WL as an independent variable for size-adjusted contrasts the following factors were found after stepwise discriminant analyses: MSW, AL and WL (Table 5). These variables were independently analyzed using covariance analyses. Queens and workers differed significantly in slope in MSW (F = 10.31, $P = 0.002$), and AL (F = 4.15, $P = 0.04$).

Generalized Mahalanobis distance (D^2: Anderson, 1968) was statistically significant ($D^2 = 2.85$; F = 6.06, $P = 0.008$) indicating slight but significant differences between the castes. In fact, comparisons between predicted and observed classifications showed that workers were 97.83% correctly classified by the method and queens were 50% correctly classified.

Colony V

Among the relationships of the averages of the five analyzed characters in queens and workers (Table 6), there were no statistically significant differences between queens and workers (*t*-test, $P < 0.05$) in colony V of *C. communis* (Fig. 3.5).

Results of the stepwise discriminant analysis based on the five characters also showed absence of differences between the castes. Using the forward procedure for stepwise discriminant analysis using castes as the grouping variable, any variable was included in the model, indicating that any character employed would explain the variation equally well.
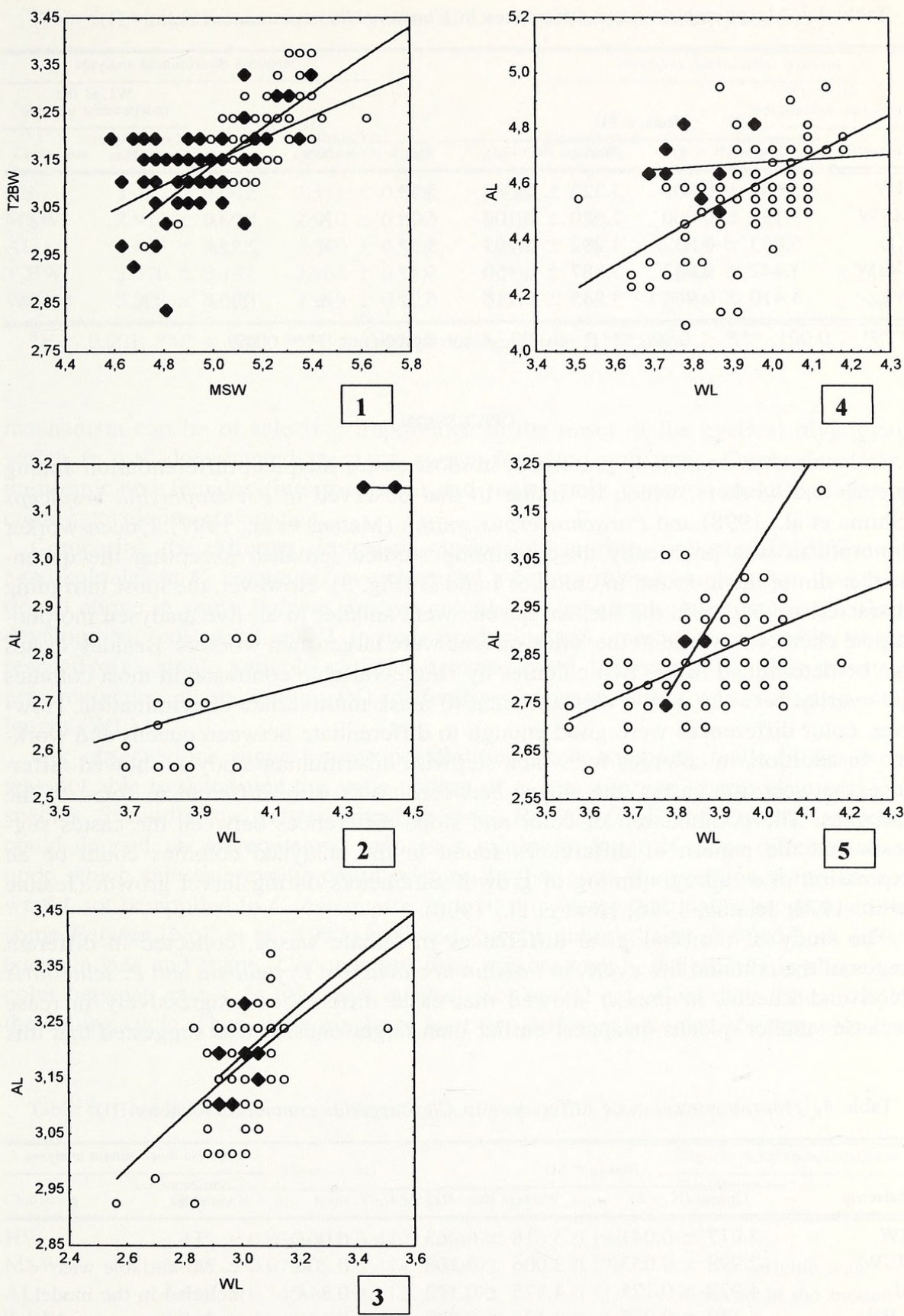
Fig. 3.   Discrimination between queens and workers of *Chartergellus communis* in colonies 1, 2, 3, 4 and 5 respectively, based on the two most discriminant characters. Black diamonds = queens, white circles = workers.

Table 3.   Morphometric caste differences in *Chartergellus communis* (Colony II).

| Characters | Means ± SD | | t-test | Stepwise discriminant analyses | | WL as the independent variable | |
	Queens (N = 2)	Workers (N = 18)		Contributor variables	F	Contributor variables	F
HW	3.645 ± 0.001	3.322 ± 0.088	5.1*				
MSW	3.150 ± 0.000	2.670 ± 0.107	6.2*	X	1.23#		
AL	5.063 ± 0.032	4.282 ± 0.195	5.5*	X	2.22#		
T$_2$BW	3.442 ± 0.032	2.887 ± 0.150	5.1*				
WL	4.410 ± 0.064	3.845 ± 0.116	6.7*	X	7.85#	X	1.32#

*$P < 0.001$, **$P < 0.02$, ***$P < 0.05$, # not significant ($P > 0.05$).

DISCUSSION

Chartergellus communis presented, in most cases, incipient differentiation among queens and workers, which is similar to that observed in *Pseudopolybia vespiceps* (Shima et al., 1998) and *Parachartergus smithii* (Mateus et al., 1997). Queen-worker dimorphism was practically absent among studied females, excepting the queen-worker dimorphism found in colonies I and II (Fig. 3). However, the most intriguing characteristic is that in the former, queens were smaller in all five analysed morphological characters while in the latter, queens were larger than workers. Besides, castes can be determined in the two colonies by single-variable contrasts, in most colonies the overlap between castes was sufficient to mask multivariate discrimination. However, color differences were good enough to differentiate between queens and workers. In addition, in colonies for which stepwise discriminant analysis showed differences between the castes, the slopes between castes were different in some of the variables. The combination of color and slope differences between the castes suggests that the pattern of differences found in the analyzed colonies could be an expression of a reprogramming of growth parameters during larval growth (Jeanne et al., 1974; Jeanne, 1996; Hunt et al., 1996).

The study of morphological differences in female wasps, collected in different stages of the colonial life cycle, in *Polybia occidentalis, P. paulista* and *P. scutellaris* (Noll and Zucchi, in press.) showed that caste differences progressively increase because smaller queens disappear earlier than larger ones. It was suggested that this

Table 4.   Morphometric caste differences in *Chartergellus communis* (Colony III).

| Characters | Means ± SD | | t-test | Stepwise discriminant analyses | |
	Queens (N = 8)	Workers (N = 93)		Contributor variables	F
HW	3.617 ± 0.041	3.618 ± 0.065	0.06#		
MSW	2.998 ± 0.053	3.006 ± 0.106	0.20#	No variable was	
AL	4.928 ± 0.125	4.875 ± 0.172	−0.84#	included in the model.	
T$_2$BW	3.189 ± 0.070	3.176 ± 0.087	−0.42#		
WL	4.224 ± 0.074	4.237 ± 0.126	0.28#		

Not significant ($P > 0.05$).

Table 5.   Morphometric caste differences in *Chartergellus communis* (Colony IV).

	Means ± SD			Stepwise discriminant analyses		WL as the independent variable	
Characters	Queens (N = 8)	Workers (N = 92)	t-test	Contributor variables	F	Contributor variables	F
HS	3.487 ± 0.042	3.511 ± 0.076	0.88#				
MSW	2.914 ± 0.047	2.910 ± 0.090	−0.12#	X		X	
AL	4.663 ± 0.115	4.580 ± 0.179	−1.28#	X	6.94**	X	
T_2BW	2.970 ± 0.132	2.964 ± 0.118	−0.20#		1.06#		8.25**
WL	3.808 ± 0.090	3.939 ± 0.127	2.84#	X	17.76#		2.29#

*$P < 0.001$, **$P < 0.02$, ***$P < 0.05$, # not significant ($P > 0.05$).

mechanism can be of selective importance in the onset of the cyclical olygogyny, which is well-documented in many swarm-founding polistines. Ovary-developed, uninseminated females (intermediates) and males only occurred at later stages of colony developmental cycles.

Comparing the different groups of queens and workers collected in differently aged colonies in *C. communis,* we observed a pattern more complex than that mentioned above in some *Polybia*. In two colonies in apparently later stages of colony development (colonies I and II, in male producing and emergence of workers phase, respectively), single variable statistics detected caste differences. In other colony in pre-emergence phase (colony IV), differences between castes were found in wing length (WL).

Our observations suggest some possibilities. First, sampling made in this work was not able to determine the same pattern of queen selection observed in previous species. Secondly, the pattern found in some *Polybia* (Noll and Zucchi, in press.) could depend on prerequisites, such as a minimum level of caste differentiation, upon which selective events could operate. In that case, the mentioned mechanism would not be applied to *C. communis*. In fact, this seems reasonable because, unlike some *Polybia* (Noll et al., 1997; Noll and Zucchi, submit.) that showed both differences in size and shape, *C. communis* does present mainly differences in shape and color between castes. In this case, queens' size would not affect their fitness during the colony cycle. Thus, there maybe at least two different schemes of queen selection

Table 6.   Morphometric caste differences in *Chartergellus communis* (Colony V).

	Means ± SD			Stepwise discriminant analyses	
Characters	Queens (N = 3)	Workers (N = 87)	t-test	Contributor variables	F
HW	3.435 ± 0.026	3.440 ± 0.064	0.15#		
MSW	2.835 ± 0.078	2.844 ± 0.092	0.17#	No variable was	
AL	4.440 ± 0.145	4.512 ± 0.172	0.71#	included in the model.	
T_2BW	2.925 ± 0.045	2.889 ± 0.103	−0.61#		
WL	3.825 ± 0.045	3.865 ± 0.119	0.57#		

Not significant ($P > 0.05$).

in epiponines during cyclical oligogyny: size dependent or not. In the former larger queens would preferentially survive versus smaller ones, while in the latter case the size of the queens is an independent trait.

Another explanation, previously suggested by Noll and Zucchi (in press), suggests that differences between castes found in some colonies and not in others from the same species could indicate that during the colony cycle new queens produced would be morphologically distinct from their mothers. However, such possibility needs an extensive analysis of colonies during the whole cycle.

Intermediate females were found in two colonies with different numbers of queens (21% and other 0.8% of the population, in colonies I and V, respectively). These results are different from certain species of *Polybia* in which intermediates were found especially in colonies with a low number of queens (Noll and Zucchi, in press), and in *Protopolybia exigua* (F. B. Noll, unpub.) and *Brachygastra mellifica* (Hastings et al., 1998), in which intermediates were always found. The intermediates' presence demonstrates that control of the ovarian development, possibly by the queens, is quite flexible at some stages of the colonial cycle, being more effective during oligogyny.

As stated by Richards (1978): "In many species a few or even (*Protopolybia, Brachygastra,* some *Polybia*) many intermediates occur with the ovarioles slightly enlarged. In other characters the intermediates are sometimes more like workers, sometimes more like queens and while their significance is uncertain it seems likely that they may have different origins, perhaps as suppressed queens or as egg-laying workers, or perhaps even, in some cases, as a stage in the development of queens." Such a characterization seems reasonable, especially because some of the possible groups were clearly observed:

1—The presence of intermediates similar to workers was observed in *Protopolybia* (Noll et al., 1996) and *Brachygastra mellifica* (Hastings et al., 1998). In these species, intermediates are found during the whole colonial cycle. In this case, queen control on workers' ovary-development seems to be highly flexible. In addition, because male production is apparently completely controlled by queens (Hastings et al., 1998), intermediates' eggs could be used for trophic purposes (Shima et al., 1998). Intermediates similar to workers were found also in some *Polybia* species (Noll and Zucchi, in press), however, in this case, intermediates appear only at the final stage of the colonial cycle, usually when only a few queens (sometimes just one queen) are present in the colony. Workers' ovary development, in this case, could reflect the loss of dominance in the colony as observed in some species of *Bombus* (Sakagami, 1976). Even though no male production analyses were performed, male production by intermediates (Richards, 1971) cannot be discarded because, in *Polybia paulista* (Noll and Zucchi, in press), a large number of males were found under oligogyny. This case differs from the results obtained in *Parachartergus colobopterus* (Strassmann et al., 1998), in which male production would occur during high queen number in order to accommodate workers interests, according to kin selection proposals.

2—The presence of queen-like intermediates or uninseminated queens was recorded in *Polybia dimidiata* (Shima et al., 1996b; Maule-Rodrigues et al., 1974); *Agelaia vicina* (Sakagami et al., 1996; Baio et al., 1998) and *Polybia occidentalis* (Noll et al., in prep.). Such intermediates can be interpreted as young queens or uninsemi-

nated queens with low reproductive potential. However, their role in social regulation in the colony remains speculative.

3—In *Pseudopolybia vespiceps* (Shima et al., 1998), *Parachartergus smithii* (Mateus et al., 1997), *P. colobopterus* (Strassmann et al., 1998) and *Chartergellus communis* (present data) caste differences are absent, either morphologically, or physiologically. In this case, all individuals could have, in some way, the possibility of reaching "reproductive status" as previously proposed by Forsyth (1978), at least in male production. In fact, that possibility cannot be discarded, because seven intermediates with queen-like ovary status were found in colony I in a male producing phase (see *Ovarian development*). In this connection, it is important to mention that peculiar life-cycle of the neotropical *Bombus atratus*, relies on two kinds of intermediate females, namely unmated (male producing), and mated females. Moreover, potential perennial traits of the colonies, exclusively depends on the latter kind of intermediates, because these can restart female's production especially at the close of mother-queen's reproduction period, and right after the queen's premature death, as well (Zucchi et al., 1996).

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