

Research Article

Morphological Caste Differences in Three Species of the Neotropical Genus *Clypearia* (Hymenoptera: Polistinae: Epiponini)

Giovanna Tocchini Felippotti,¹ Lucas Mateus,¹ Sidnei Mateus,¹ Fernando Barbosa Noll,² and Ronaldo Zucchi¹

¹Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Av. Bandeirantes, 3900, 14040-901 Ribeirão Preto, SP, Brazil

²Departamento de Botânica e Zoologia, Instituto de Biociências, Letras e Ciências Exatas, UNESP, Rua Cristóvão Colombo, 2265, 15054-000 São José do Rio Preto, SP, Brazil

Correspondence should be addressed to Giovanna Tocchini Felippotti, gio_tf@yahoo.com.br

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Clypearia is a rare genus of swarm-founding Neotropical wasp whose biology is very little known. Morphological castes differences, condition of ovaries, relative age, and color pattern differences were analyzed in three species of *Clypearia*. Physiological differences and low morphometric differentiation between queens and workers were present in all species studied, indicating that these species are characterized by “physiological caste only”. We suggest that caste determination in the three *Clypearia* species studied is postimaginal.

1. Introduction

Swarm-founding polistine wasps belong to the tribe Epiponini and are represented by 19 genera [1] with at least 229 species ecologically dominant in the Neotropical region [2]. The most remarkable characteristic of the Epiponini wasps is nest foundation by the swarming of a large number of individuals including workers and queens [1]. In some species there is slight differentiation between castes [3–6]. However, there are species in which queens are significantly larger or smaller than workers in some morphological characters [2, 7, 8]. Noll et al. [2] proposed the following groups: (1) casteless: no size or shape difference associated with reproduction, and all females largely develop ovaries; (2) physiological caste only: no morphometric differences, but ovarian condition unambiguous by the sterility of all workers; (3) queens larger but mostly the same shape; and (4) queens shaped differently with some measures smaller than workers.

In association with this variation in the patterns of caste distinction, there is the presence of unseminated females which have developed ovaries named “intermediates” [3] because they usually occur more frequently in species with low caste differentiation [2]. According to Mateus [9], intermediates of *Parachartergus fraternus* are active workers “scouts” during the swarm, that build envelope, sometimes work as a foragers, and lay eggs during colony initiation. The presence, distribution, and occurrence (or not) of intermediate females in several levels of colony cycles organized the social wasps according to five different types of social regulation [8], and in some species the differences between females progressively increase during the colonies ontogenetic development. All these patterns provide to tribe Epiponini a status of prominence in sociobiology [10].

Clypearia was first described as subgenus of *Polybia* for the species *P. apicipennis* [11] and *apud* [12]. *Clypearia* occurs from Mexico to Brazil. In Brazil seven species are found and three are endemic. The cells of the nest are

constructed directly on the substrate and present hidden envelope. According to some authors [12–14] these nests are associated with ants of the genus *Azteca*. The nest of these species was described by Ducke [15], noting its similarity to that of the genus *Synoeca*. Ducke [16] raised *Clypearia* to genus [13], in part because of nest architecture, grouping *Clypearia* with *Synoeca* and *Metapolybia* rather than *Polybia* [12]. After some morphological analysis, Carpenter et al. [12] established that *Occipitalia* is a synonymy of *Clypearia*. According to Noda et al. [17], caste differences in *Synoeca cyanea* are clearly discriminated by physiology but not by morphology. Using morphometric analyses and multivariate statistics, it was found that caste differences in *Metapolybia docilis* are slight but more distinct in latter stages of the colony cycle [18]. Because *Clypearia* is related to these genera there is a possibility that caste syndrome for this genus is similar to that found in *Synoeca* and *Metapolybia*.

The species of genus *Clypearia* are rare [13], and little is known about its biology. This work intends to describe the caste patterns in three species of the genus and to show some possibilities of social organization in this group.

2. Material and Methods

For this study, five colonies of genus *Clypearia* were used: three of *C. sulcata*, de Saussure, 1854, one of *C. duckei*, Richards, 1978, associated with a nest of *Azteca*, both collected in municipal district of Presidente Figueiredo – Amazonas state, Brazil (S- 01° 48' 802''; W- 060° 07' 185'') and one of *C. angustior*, Ducke, 1906 collected in the municipal district of Paraibúna – São Paulo state, Brazil (S- 23° 22'; W- 045° 39'). The nests were collected using plastic bags with paper towels soaked in ether. All adult wasps from each colony were preserved in ethanol 95% immediately after collection. Even though the study of several colonies is beneficial in terms of obtaining additional information on colony cycles [7], the information gained from examining a single colony provides important and useful information regarding caste syndromes and is an important starting point for future studies [2].

Castes were defined based on ovarian development and insemination of spermatheca. Queens were defined as ovarian-developed females bearing sperm in the spermatheca, and workers were defined as unmated females without ovarian development [10, 19].

In order to verify insemination, the spermatheca was removed and put on a slide bearing a drop of acid fuchsine solution (1 : 1), and the presence of sperm cells was detected under a microscope. According to Richards [20] and West-Eberhard [21], the relative age of all adult females can be estimated in three crescent classes, analyzing the pigmentation of the transverse apodeme across the hidden base of the fifth sternum, as follows: without pigmentation or incipient (1); light brown (2) and dark brown (3). For morphometric analysis, all females of each colony were studied, because these colonies are few in population. Measurements were taken for 7 morphometric variables in each female: head width (LC); minimum interorbital distance (DmI); gena width (LG); mesoscutellar width (LM); alitrunk length (CME); basal width of tergite II (LBT₂); partial length of the forewing (CA).

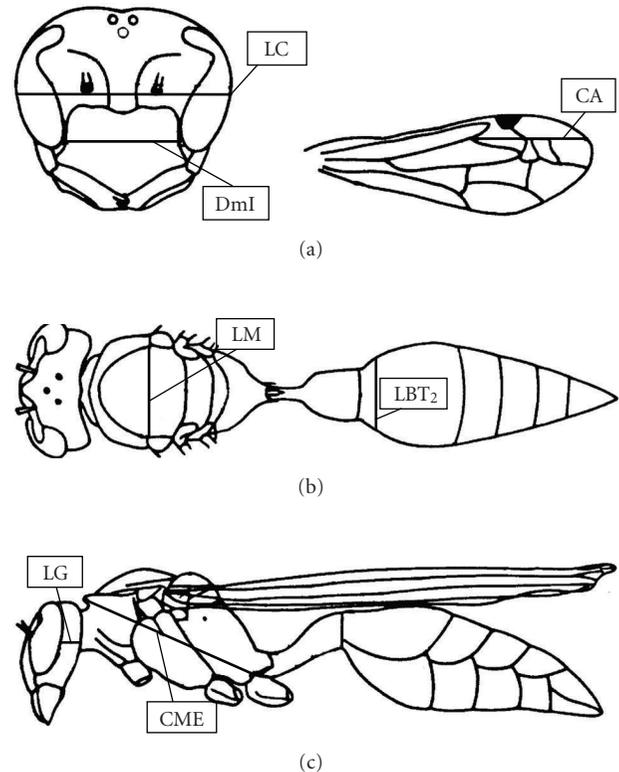


FIGURE 1: Representative measures for morphometric analyses: head width (LC); minimum interorbital distance (DmI); gena width (LG); mesoscutellar width (LM); alitrunk length (CME); basal width of tergite II (LBT₂); partial length of the forewing (CA). Modified by Shima et al. [22].

width (LG); mesoscutellar width (LM); alitrunk length (CME); basal width of tergite II (LBT₂); partial length of the forewing (CA) (Figure 1), using a stereomicroscope, digital camera, and measure software.

For the statistical analysis, females were divided in two groups: queens and workers. Means and standard deviations were calculated using one-way ANOVA. A stepwise discriminant analysis was used to identify the character most significant that contributes to caste distinction. After, the most discriminant characters were plotted for caste discrimination, the Wilks' Lambda was used to determine the degree to which separate measures contributed to final model. This is an alternative to the use of an *F* to remove at each step. Variables that appear in final model but do not have significant *F* ratios represent variance components that are explained by some combination of the other variables also in the model and therefore no longer contribute to discrimination itself. Wilks' Lambda varies from zero to one; the lower the value, the greater the significance. In order to check the test efficiency, a classification matrix test was used to check the number and percent of correctly classified cases in each group [8]. The data were computed using the "STATISTICA 6.0 Statsoft" software.

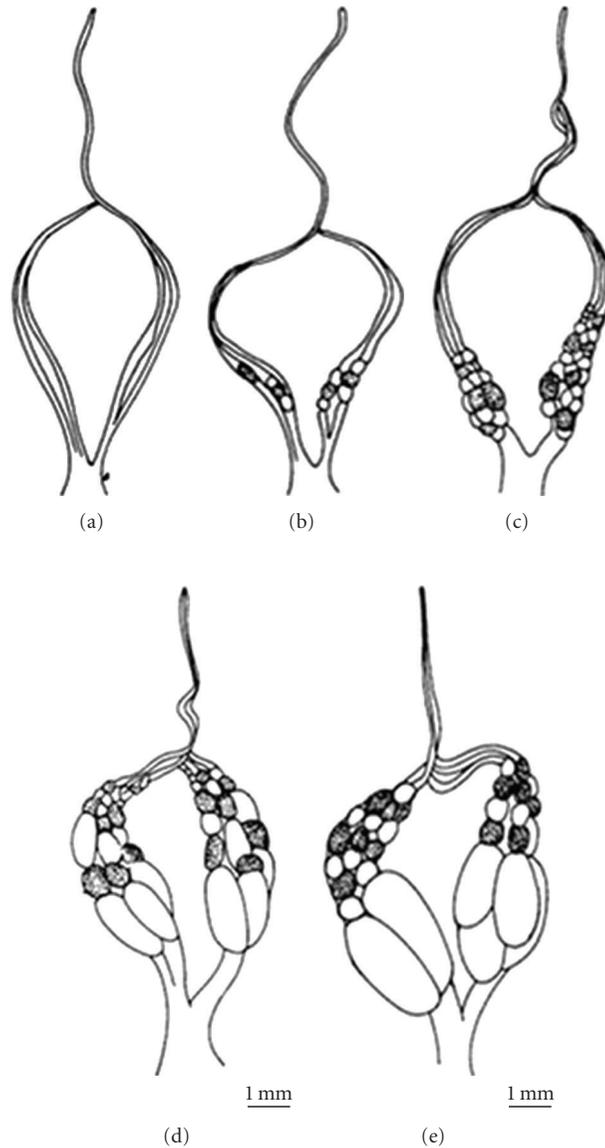


FIGURE 2: Grades of ovarian development found among females in colonies of *Clypearia*. Type (a), (b) and (c): workers; Type (d) and (e): queens.

3. Results

3.1. Ovarian Development and Insemination. The number of ovarioles was three in each ovary, as found in other Polistinae, and the ovarian development was classified according to five categories (Figure 2): Type (a): filamentous ovarioles bearing no visible oocytes, Type (b): possessed slightly developed oocytes, Type (c): small well-defined oocytes, Type (d): possessed at least one near mature oocyte, and Type (e): well-developed oocytes. In the *C. sulcata* colonies, we found all types of ovaries, except Type (d). In *C. duckei* all types of ovaries were found and in *C. angustior* there were found all types of ovaries, except Type (c) (Figure 2; Table 1). Insemination was found in females with Type (d) and (e) ovaries.

3.2. Relative Age. In relation to females age, colony I of *C. sulcata* presented workers in young and median age, and the single queen showed median age. In colony II of *C. sulcata*, queens showed median age, and the workers were found in all age patterns. Colony III of *C. sulcata* presented all queens as young females and workers as median and old females. In colony of *C. angustior*, queens and workers were old females, except one worker that had median age. In colony of *C. duckei* queens and workers females were found in all age patterns; however most queens were younger and most workers were older (Figure 3).

3.3. Morphometric Analysis. Among the colonies of *C. sulcata*, colony I showed two characters (LC and LG) statistically

TABLE 1: Ovary development for all species analyzed in the genus *Clypearia*.

Species	Colony characteristics	N Females	Ovaries (%)				
			A	B	C	D	E
<i>C. sulcata</i> I	Swarm	23	30.4	39.1	26.1	0	4.4
<i>C. sulcata</i> II	Work production	25	56	16	20	0	8
<i>C. sulcata</i> III	Work production	50	66	14	14	0	6
<i>C. angustior</i>	Male production	14	28.6	21.4	0	14.3	35.7
<i>C. duckei</i>	Work production	119	28.6	10.1	45.4	0	16

TABLE 2: Means, standard deviations, and *F* values of ANOVA for the analyzed colonies of the genus *Clypearia*.

(a)									
Colony	<i>C. sulcata</i> I			<i>C. sulcata</i> II			<i>C. sulcata</i> III		
			Bonferroni			Bonferroni			Bonferroni
Characters	Queen	Worker	<i>t</i> -test	Queen	Worker	<i>t</i> -test	Queen	Worker	<i>t</i> -test
	(<i>N</i> = 1)	(<i>N</i> = 16)	Q/W	(<i>N</i> = 2)	(<i>N</i> = 23)	Q/W	(<i>N</i> = 3)	(<i>N</i> = 47)	Q/W
HW	2.97 ± 0.00	3.13 ± 0.05	**	3.19 ± 0.01	3.16 ± 0.03	#	3.12 ± 0.06	3.16 ± 0.06	#
IDm	1.19 ± 0.00	1.24 ± 0.03	#	1.28 ± 0.01	1.27 ± 0.02	#	1.26 ± 0.04	1.23 ± 0.03	#
GW	0.48 ± 0.00	0.55 ± 0.03	**	0.56 ± 0.00	0.59 ± 0.04	#	0.54 ± 0.03	0.55 ± 0.02	#
MSW	1.90 ± 0.00	2.00 ± 0.06	#	2.06 ± 0.01	2.04 ± 0.05	#	1.97 ± 0.03	2.00 ± 0.06	#
AL	3.86 ± 0.00	4.02 ± 0.11	#	4.18 ± 0.04	4.18 ± 0.07	#	4.06 ± 0.13	4.03 ± 0.10	#
T2BW	1.31 ± 0.00	1.37 ± 0.04	#	1.37 ± 0.03	1.37 ± 0.05	#	1.34 ± 0.03	1.34 ± 0.05	#
WL	1.50 ± 0.00	1.56 ± 0.11	#	1.65 ± 0.01	1.62 ± 0.08	#	1.58 ± 0.04	1.59 ± 0.05	#

(b)						
Colony	<i>C. angustior</i>			<i>C. duckei</i>		
			Bonferroni			Bonferroni
Characters	Queen	Worker	<i>t</i> -test	Queen	Worker	<i>t</i> -test
	(<i>N</i> = 7)	(<i>N</i> = 7)	Q/W	(<i>N</i> = 16)	(<i>N</i> = 112)	Q/W
HW	2.88 ± 0.04	2.78 ± 0.08	**	2.95 ± 0.05	2.95 ± 0.05	#
IDm	1.21 ± 0.02	1.14 ± 0.03	*	1.18 ± 0.03	1.15 ± 0.03	**
GW	0.42 ± 0.04	0.39 ± 0.03	#	0.34 ± 0.02	0.35 ± 0.03	#
MSW	2.01 ± 0.05	1.90 ± 0.10	***	2.26 ± 0.07	2.21 ± 0.06	**
AL	4.28 ± 0.09	4.07 ± 0.19	**	4.51 ± 0.19	4.43 ± 0.12	***
T2BW	1.34 ± 0.06	1.31 ± 0.03	#	2.03 ± 0.08	1.94 ± 0.06	*
WL	1.80 ± 0.06	1.69 ± 0.09	**	1.59 ± 0.10	1.58 ± 0.10	#

P* < .001; *P* < .02; ****P* < .05; # not significant (*P* > .05).

smaller in queens compared with workers colonies II and III presented no significant different character (Table 2). The colony of *C. angustior* showed five characters (LC, DmI, LM, CME, and CA) statistically larger in queens compared to workers. Colony of *C. duckei* showed four characters (DmI, LM, CME, and LBT2) statistically larger in queens than in workers (Table 2).

According to multivariate analyses, LG, DmI, and LC were predominant in the discrimination models (Table 3). High values of Wilks' Lambda (above 0.8; Table 3) for colonies of *C. sulcata* II and III and *C. duckei* indicate low power of discrimination of castes, and in the colony of *C. angustior*, the Wilks' Lambda values were lower (below 0.4;

Table 3), that could be a better discriminator between castes. However, when we looked at the values of *P* for this colony, we observed that the values were not statistically significant. Thus, no single character could discriminate caste in these colonies. Such differences suggest that variation during the colony cycle occurs in other epiponines [7, 8].

Group comparisons after discriminant analysis showed queens and workers as well-defined groups in latter stages of the colony cycle as found in *Metapolybia docilis* [18], indicating a high overlap between castes in morphological characters (Table 4; Figure 4).

Color pattern differences were observed between queens and workers in areas of light coloration: in the gena, clypeus,

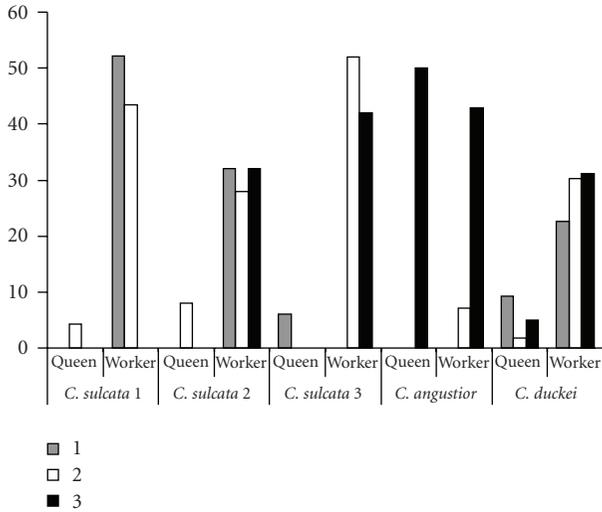


FIGURE 3: Relative age based on the pigmentation of the 5th gastric sternite of queens and workers in species of genus *Clypearia*. (1) Without pigmentation or incipient; (2) little brown; (3) dark brown.

TABLE 3: Discrimination between queens, workers, and intermediate females in all analyzed colonies of genus *Clypearia* after forward stepwise discriminant function analyses.

Colony	Character	Wilks' Lambda	P
<i>C. sulcata</i> II	GW	0.96	.08
	HW	0.94	.11
	IDm	0.98	*
<i>C. sulcata</i> III	HW	0.90	*
	MSW	0.77	.21
	IDm	0.60	*
<i>C. angustior</i>	T2BW	0.27	.42
	WL	0.35	.10
	GW	0.30	.26
<i>C. duckei</i>	T2BW	0.87	*
	IDm	0.78	*
	HW	0.75	*
	GW	0.71	.03

* $P < .01$.

and hind margin of pronotum. In the workers these marks are strong yellow while in queens are light yellow to near white. These patterns are the same for all species studied (Figure 5).

4. Discussion

Size differentiation is considered as an initial step for the origin of morphological castes in the three main groups of social Hymenoptera. In social wasps, the differences are more conspicuous in Vespinae and more complex in Polistinae [2].

According to ovarian development, we observed that in colonies of *C. sulcata* and *C. duckei* Type (d) ovary was not found (Figure 2; Table 1). However, pattern (d) was found

TABLE 4: Classification matrix queens, workers, and intermediate females in all analyzed colonies of genus *Clypearia* after discriminant function analyses.

Colony	Observed classification	Predicted classification		Corrected classified females (%)
		Queen	Worker	
<i>C. sulcata</i> II	Queen ($n = 2$)	0	2	0
	Worker ($n = 23$)	1	22	95.7
<i>C. sulcata</i> III	Queen ($n = 3$)	2	1	66.7
	Worker ($n = 47$)	0	47	100
<i>C. angustior</i>	Queen ($n = 7$)	7	0	100
	Worker ($n = 7$)	1	6	85.7
<i>C. duckei</i>	Queen ($n = 16$)	9	7	56.3
	Worker ($n = 112$)	3	96	97

in *C. angustior*, and type (c) ovaries were not found, unlike all other colonies (Table 1). This may be due to phase of colony cycle for each colony. Indeed, in contrast to our data, Noll et al. [2] did not find females with Type (c) ovaries in colony *C. sulcata*, and perhaps this colony was in the phase of male and gyne production like the *C. angustior* colony studied here.

In all colonies, except colonies II and III of *C. sulcata*, at least two measures were statistically different between castes (Table 2). In *C. sulcata* II and *C. sulcata* III no character had statistical difference (Table 2). Because some colonies showed more significant differences among morphological characters, we suggest that the colonies studied here showed slight differences in morphology (Figure 4).

Based on discriminant analysis, small differences were found. The high values of Wilks' Lambda (Table 3) support this result. Indeed, *C. angustior* showed low Wilks' Lambda values (Table 3) perhaps due to phase of colony cycle. The absence of morphological and physiological caste differences was found in *Protopolybia acutiscutis* cited as *P. pumila* [23], *P. exigua exigua* [24], *Parachartergus smithii* [25], *Pseudopolybia vespiceps* [26], *Polybia chrysothorax*, *P. jurinei*, *Parachartergus fraternus*, *Angiopolybia spp*, *Chartergellus communis* [3, 10, 27], *Brachygastra scutellaris* [28], *B. lecheguana* [29, 30], *B. mellifica* [31], *Protopolybia chartergoides* [32], and *Metapolybia docilis* [18].

Based on relative age of adult females and absence of males (Figure 3), it is possible to suggest that all colonies of *C. sulcata* and the single colony of *C. duckei* were producing workers, and *C. angustior* colony was producing males and new queens (Figure 3; Table 1). According to group comparisons (Table 4), only *C. angustior* colony showed a

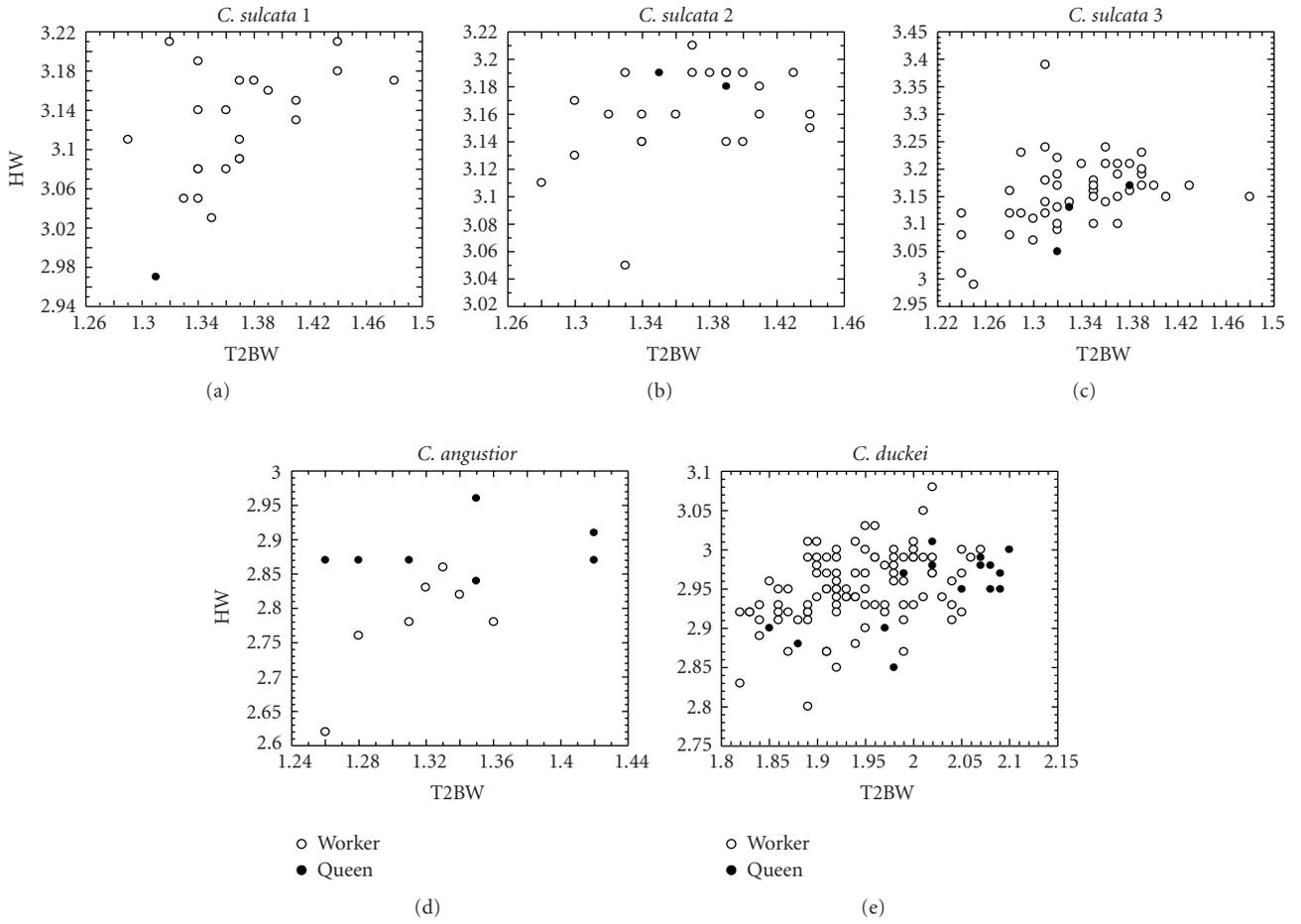


FIGURE 4: Caste discrimination in the analyzed colonies of *Clypearia* based on the multivariate analyses.

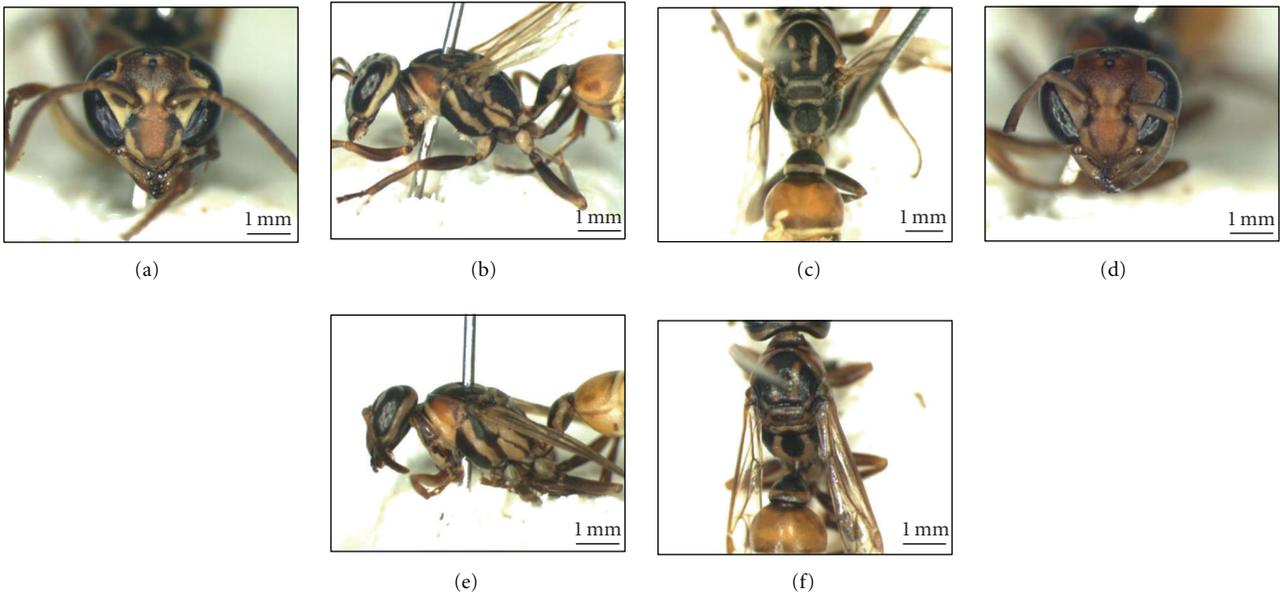


FIGURE 5: Color patterns: (a–c): view of worker; (d–f): view of queen.

good discrimination that could be because all queens were in a more advanced relative age (Figure 3).

The differentiation between queens and workers was found when color of head and mesosoma was compared (Figure 5). According to Shima et al. [22], color pattern differs between queens and workers of *Apoica flavissima*, as observed in *Polybia dimidiata* [33], *Parachartergus smithii* [25], *Chartergellus communis* [27], and various *Polybia* species of the subgenus *Myrapetra*, as *P. diguetama*, *P. occidentalis*, *P. platycephala sylvestris*, *P. scrobalis surinama*, and *P. scutellaris* [13].

The absence of morphological differences is shown to be ancestral condition for Epiponini [2, 34]. Noll et al. [2] grouped *Clypearia* with *Synoeca* and *Metapolybia* plus *Asteloeca* and proposed that these genera belonging to a pattern called “physiological caste only”, meaning that no morphometric differences but ovarian condition unambiguous by absence of type (c) females were present. Our data agree with these conditions. So, we can suggest that due to low morphological differentiation, the castes in species of *Clypearia* studied here are determined postimaginally [8, 10] probably due to reprogramming of growth parameters [35] and maybe the size has an important role during the process of queen elimination during the cyclical oligogyny [8].

Acknowledgments

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