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Caste differences in *Pseudopolybia compressa* (Hymenoptera: Vespidae: Polistinae)

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ABSTRACT. Studies of morphological caste syndromes in the tribe Epiponini help us to understand the evolution of social behavior in insects. Few studies have integrated morphological syndromes of various species from the same or distinct genera. We studied morphological differences between castes from three colonies of *Pseudopolybia compressa* de Saussure, 1854, in order to relate their caste syndrome with those of other species in the genus. We took eight morphometric measures and females were classified in relation to ovarian development and spermathecal contents. Females of Colony 1 (C1) present a higher distinction between castes than females of Colonies 2 and 3 (C2 and C3), and, in general, queens of the three colonies are larger than workers in some measures but smaller in others. In *Pseudopolybia* Dalla Torre, 1894, shape rather than size is a more important trait in caste divergence.

KEY WORDS. Dimorphism; Epiponini; morphological syndromes; queen; shape; workers.

Studies of morphological castes in social wasp (Hymenoptera: Vespidae) are important for understanding the evolution of social behavior in insects. The great variability that these wasps show in their social organization suggests different evolutionary strategies (Noda *et al.* 2003, Noll *et al.* 2004; Noll & Wenzel 2008). Polistine wasps are especially interesting because some species have morphological and physiological caste differentiation, meanwhile others only differ in their behavior (Noll *et al.* 2004). Epiponini, a Neotropical tribe of Polistinae, presents morphological and behavioral variation between species. As reviewed in Noll *et al.* (2004), there are basically four syndromes: 1) no morphological differences among females, 2) egglayers (queens) larger than workers, with intermediates in both morphometric and ovarian development aspects, 3) females either with ovaries developed or not (but possibly with spermatheca empty even if ovaries are developed), and 4) egglayers different from workers in shape, with smaller head and larger abdomen than workers. There are only a few comparative studies integrating morphological syndromes of various species either across the tribe (Noll *et al.* 2004) or within the same genus (Andena *et al.* 2007).

It is important to understand what is happening within species and between species of the same genus because there are several factors that could generate changes in social organization or in morphological caste syndromes, such as colony cycle (West-Eberhard 1978, Noll & Zucchi 2002), colony size (Karsai & Wenzel 1998, Bourke 1999), altitudinal distribution (Rodríguez & Sarmiento 2008), and nutritional differences during larval development (West-Eberhard *et al.* 1995).

Pseudopolybia Dalla Torre, 1894 is a small genus of Vespidae with four species that are taxonomically problematic (Andena *et al.* 2007). Jeanne (1996) found queen-worker dimorphism in *Pseudopolybia difficilis* Ducke, 1905 in some measures but not in the overall size, generating different shapes. Shima *et al.* (1998) found a different situation in *Pseudopolybia vespiceps* de Saussure, 1864, where caste dimorphism is less pronounced than in *P. difficilis*, but queens and workers had two different patterns of growth rate. These two works show how variable morphological syndromes can be in the same genus. In *P. vespiceps* females with well developed ovaries and no insemination were found, but the role of these intermediates in the colony is still in discussion. Morphometric analyzes (Noll *et al.* 2004) showed intermediates of some species were more similar to workers, whereas in other species they were more similar to queens. Because *Pseudopolybia* presents two different patterns of queen-worker dimorphism (see above), it is important to augment the knowledge on castes in this genus, in this way, we quantified the morphological and physiological aspects of caste in three colonies of *Pseudopolybia compressa* de Saussure, 1854.

MATERIAL AND METHODS

Morphometric measurements were taken from females of three colonies of *P. compressa*, collected in state of Mato Grosso, Brazil: colony 1 (C1) – Nova Xavantina (14°41’907”S, 52°21’014”W), 7/XII/2006, colony 2 (C2) – Ribeirão Cascalheira (12°57’929”S, 51°49’605”W), 26/XI/2006, and colony 3 (C3) – Nova Mutum (13°51’903”S,56°11’619”W), 23/VII/2000. For each colony, measurements from 50 non-reproductive females (workers) and 30 reproductive females (queens) were taken. Females were classified in relation to ovarian development and spermathecal contents. The presence of sperm cells in the spermatheca was detected by observation under the microscope. Eight measurements were taken from external body parts including head [head width (HW), minimum interorbital distance (IDm)], mesosoma [width of mesoscutum (MSW), alitrunk length (AL)] and metasoma [basal height of metasomal tergite I (T_1BH), length of tergite I (T_1L), basal widths of tergite II (T_2BW) and length of the cubital cell of the forewing (WL)]. Data were statistically analyzed by Discriminant Function Analysis and ANOVA with Bonferroni's a posteriori *t*-test using Statistica software.

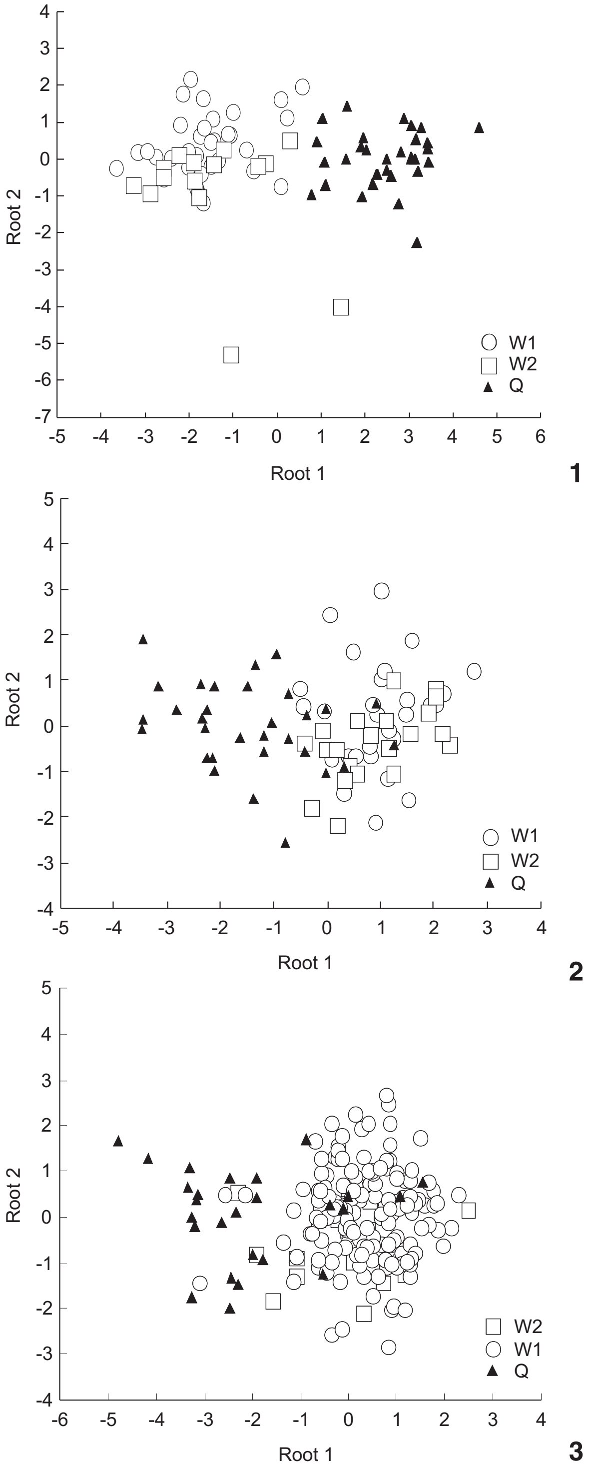
RESULTS

We found four stages of ovarian development: stage 1 – with filamentous ovarioles without visible oocytes; stage 2 – with young or very small oocytes; stage 3 – with one or more mature oocytes in each ovariole and the spermatheca is empty; stage 4 – with long and well developed ovaries, with at least one mature egg in each ovariole and the spermatheca is inseminated (see Mateus *et al.* 1997 for details). Stage 3 was found only in one female from C1 and two from C2. Because of such reduced number of females with this kind of ovary we classified females in three categories: Workers 1 – with ovaries on stage 1, Workers 2 – with ovaries on stages 2 or 3, and Queens – with ovaries on stage 4.

Nest contents of C1 included eggs, larvae and a small number of pupae. We found 100 queens and 1824 workers. According to Discriminant Function Analysis, females of C1 were clearly separated by morphology with Wilks' lambda values close to 0.2, a value high enough to discriminate castes in other and better known species (Noll *et al.* 2004). Castes were separated by five of the eight measured characters: AL, MSW, T_1BH, T_1L, and T_2BW (Tab. I and Figs 1-3). ANOVA showed that

Table I. Morphometric discriminatory variables (mm) between females of the studied colonies of *P. compressa* according to Discriminant Function Analysis.

Colony	Variable	Wilks lambda	F- remove (2.71)	Probability
I	MSW	0.209	8.787	p < 0.001
	T2BW	0.207	8.495	p < 0.001
	AL	0.194	5.771	p < 0.050
	T1BH	0.210	9.194	p < 0.001
	T1L	0.206	8.194	p < 0.001
	HW	0.465	6.203	p < 0.050
II	IDm	0.489	8.371	p < 0.001
	T1BH	0.437	3.701	p < 0.050
	T2BW	0.570	10.000	p < 0.001
III	HW	0.540	6.430	p < 0.010
	IDm	0.530	6.020	p < 0.010



Figures 1-3. Female discrimination for colonies of *P.* compressa: (1) Colony 1; (2) Colony 2; (3) Colony 3. (Q) Queen, (W1) workers 1, (W2) workers 2. According to the Discriminant Function Analysis.

castes in C1 can be separated by the same variables of the Discriminant Function Analysis, but also by WL (F = 12.83, $p < 0.001$). Queens of C1 were in general bigger than both groups of workers in all measures of the petiole (T_1BH, T_1L and T_2BW), but smaller in the measures of the mesoscutum (AL and MSW) and in WL (Tab. II). According to Discriminant Function Analysis for C1, 97% of workers 1 were classified correctly, 13% of workers 2 were classified correctly (12 workers 2 were classified as workers 1 and one as a queen); 100% of the queens were classified correctly.

Colony 2 had 107 queens, 2676 workers and 785 males. Castes in C2 were less conspicuous if compared to C1, with higher Wilks' lambda values (meaning more ambiguity), closer to 0.4, and castes being separated only by three variables: HW, IDm and T_1BH (Tab. I and Figs 1-3). According to ANOVA, queens of C2 are also bigger than workers 1 and 2 in the measures of petiole (T_1BH and T_2BW) and in head IDm, but smaller in HW (F = 5.17, $p < 0.0001$) (Tab. II). According to Discriminant Function Analysis for C2, 64% of workers 1 were classified correctly (eight females should be classified as workers 2 and one as a queen); 28% of workers 2 were classified correctly (12 females should be classified as workers 1 and one as a queen), and 84% of the queens were correctly classified (2 should be workers 2 and 3 workers 1).

Colony 3 was composed of 1149 queens, 2079 workers, and 288 males. Morphological differences in C3 were less distinct than in C2, with higher Wilks' lambda values closer to 0.5 (Tab. I and Figs 1-3). Queens can be separated from workers 1 and 2 by three variables: HW, IDm and T_2BW. According to ANOVA queens of C3 are smaller only than workers 2, in HW and WL, and bigger than workers 1 and 2, in IDm, T_1L and T_2BW (Tab. II). According to Discriminant Function Analysis for C3, 79.2% of queens were classified correctly (seven females should be classified as workers 1); none of workers 2 were classified correctly (all females should be classified as workers 1); and 93.3% of workers 1 were classified correctly (three females should be classified as queens).

DISCUSSION

We found morphological differences between castes in *P. compressa*, and some traits resemble those found in *P. difficilis* (Jeanne 1996): queens are larger than workers in some measurements of body parts but smaller in other body parts, and there are a few intermediates in the population. In C1 and C2 there were a lower proportion of queens in the population. C1 was in a pre-emergence phase because we found eggs, larvae and a few pupae, and C2 was in a male producing phase. C3 was also in a male producing phase, but in a later stage, probably in a pre-swarming phase, because, in addition to males, there was also a high proportion of queens. According to West-Eberhard (1978), colonies of *Metapolybia aztecoides* Richards, 1978 (Vespidae) alternate between multiple queens (polygynous) and single queen (monogynous) phases. In addition, Noll & Zucchi (2000, 2002) showed that when the number of queens was low there was a higher difference between morphological castes in *Polybia occidentalis* Olivier, 1791, *Polybia paulista* H.

Table II. Mean of morphometric variables (mm) that significantly differed between queens, workers 1 and workers 2, according to ANOVA, with a posteriori test of Bonferroni, for Colony 1 of *P. compressa*. (Q) Queens, (W1) workers 1, (W2) workers 2.

Colony	Mean ± Standard Deviation				Bonferroni Test		
	Variable	Queens	Workers 1	Workers 2	Q/W1	Q/W2	W1/W2
I	MSW	2.735 ± 0.057	2.806 ± 0.073	2.782 ± 0.048	p < 0.001	p > 0.050	p > 0.05
	T2BW	2.925 ± 0.065	2.859 ± 0.099	2.819 ± 0.084	p < 0.010	p < 0.001	p > 0.05
	T1BH	2.384 ± 0.067	2.294 ± 0.109	2.304 ± 0.149	p < 0.010	p > 0.050	p > 0.05
	T1L	0.525 ± 0.038	0.473 ± 0.037	0.461 ± 0.029	p < 0.001	p < 0.001	p > 0.05
	AL	4.589 ± 0.124	4.767 ± 0.153	4.731 ± 0.138	p < 0.001	p < 0.010	p > 0.05
	WL	4.472 ± 0.100	4.662 ± 0.159	4.615 ± 0.123	p < 0.001	p < 0.010	p > 0.05
II	T2BW	3.015 ± 0.147	2.904 ± 0.085	2.919 ± 0.075	p < 0.001	p < 0.010	p > 0.05
	T1BH	2.367 ± 0.087	2.294 ± 0.091	2.295 ± 0.052	p < 0.010	p < 0.010	p > 0.05
	HW	3.295 ± 0.090	3.396 ± 0.061	3.417 ± 0.037	p < 0.001	p < 0.001	p > 0.05
	IDm	1.671 ± 0.035	1.596 ± 0.048	1.615 ± 0.057	p < 0.001	p < 0.001	p > 0.05
III	HW	5.332 ± 0.144	5.431 ± 0.140	5.419 ± 0.119	p < 0.010	p > 0.050	p > 0.05
	IDm	2.510 ± 0.077	2.404 ± 0.066	2.434 ± 0.069	p < 0.050	p < 0.001	p > 0.05
	T1L	3.587 ± 0.161	3.469 ± 0.125	3.463 ± 0.137	p < 0.050	p < 0.001	p > 0.05
	T2BW	4.725 ± 0.171	4.401 ± 0.179	4.482 ± 0.197	p < 0.001	p < 0.001	p > 0.05
	WL	7.644 ± 0.182	7.711 ± 0.162	7.658 ± 0.206	p < 0.050	p > 0.050	p > 0.05

von Ihering, 1896, *Polybia scutellaris* White, 1841, *Protopolybia exigua* de Saussure, 1854, and *Chartergus globiventris* de Saussure, 1854, which is similar to our findings: Colonies C1 and C2 presented more castes distinction (and fewer queens) than C3, which showed less distinction (but more queens).

Differences in body size proportions between queens may be related to a competitive ability. In a colony founded by swarm, the number of queens is higher (like C3, that was probably in a pre-swarming stage) and gradually declines (West-Eberhard 1978) because smaller queens could be eliminated from the colony (Noll & Zucchi 2000). This situation allows the persistence of larger queens in older colonies, and consequently a higher degree of morphological caste differences, as we found in C1 and C2 of *P. compressa*.

Although the degree of morphological variation in this study differs among the three colonies, there is a general pattern that queens are smaller than workers in some variables and larger in others. Queens of *P. compressa* are larger in petiole measures and smaller in head width and mesoscutum measures (MSW, AL and WL), which is similar to what was found in *P. difficilis* (Jeanne 1996). In the Epiponini there are lineages with this similar pattern of caste distinction, such as *Apoica* Lepeletier, 1836, (Shima *et al.* 1994, Jeanne *et al.* 1995, Noll & Zucchi 2002), several species of *Agelaia* Ducke, 1910, and *Polybia* Lepeletier, 1836, and other genera (for more details see Noll *et al.* 2004, Noll & Wenzel 2008).

The origin of morphological castes in Epiponini is controversial, probably because there is not a single origin of reproductive specialists (Noll & Wenzel 2008). In these wasps, differences in body proportions of queens relative to workers are a consequence of changes along the longitudinal body axis probably due to a different programming of growth parameters in the pre-adult stage (Jeanne *et al.* 1995). In these species, shape rather than size is a more important trait for caste divergence, and according to Jeanne & Fagen (1974) shape could be an adaptation to the social role of the individuals in the colony. However, the functions of shape differences are unknown.

Caste dimorphism in *P. vespiceps* is less pronounced than in *P. difficilis* and *P. compressa*, because in *P.vespiceps* only two characters separate castes: workers are larger than queens in the abdomen (T2BW), but have fewer hamuli on the wings (Shima *et al.* 1998). According to Andena *et al.* (2007), *P. compressa* and *P. vespiceps* are sister species based on morphological characters including male genitalia. Because the absence of caste dimorphism is plesiomorphic (Noll & Wenzel 2008), we have two possible scenarios for the origins of castes in *Pseudopolybia*: caste dimorphism has two independent origins in *P. difficilis* and in *P. compressa* or caste dimorphism is plesiomorphic for the genus with a reversal to absence of caste dimorphism in *P. vespiceps*. Even though it was not reported if intermediates are present in *P. difficilis* (Jeanne 1996), it seems obvious that ovarian activation in unmated females seems to be a widespread trait, found both in *P. vespiceps* (Shima *et al.* 1998) and *P. compressa* (present data).

In conclusion, our results reinforce that evolution of caste in Epiponini remains a difficult problem, but we are discovering large patterns that seem to operate in many species.

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