

Caste Dimorphism in the Wasp *Epipona guerini* (Hymenoptera: Vespidae; Polistinae, Epiponini): Further Evidence for Larval Determination

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ABSTRACT: Queens of the social, swarm-founding wasp *Epipona guerini* are larger than workers in each of 13 morphometric variables. Multivariate analyses revealed that 6 of the variables contribute significantly to queen-worker differentiation. Relationships among thorax length, wing length, and width of the second gastral tergite differ between queens and workers in ways that can only occur through difference in developmental pathways during larval development. Pre-imaginal caste determination has been documented in six genera of Epiponini; *Epipona* is the second of these that now has been subjected to detailed analysis that revealed caste differences that are not explained by size-based allometry.

Difference in morphology between queen and worker castes and among worker subcastes of social insects has been a focal problem in evolution since Darwin (1859) specified such differences (but not the origin of sterility and, so, not the origin of sociality) as “one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory.” Limited interchange of ideas between evolutionary theorists on one hand and empiricists exploring caste determination on the other has perhaps delayed progress on the problem (Hunt and Nalepa 1994; Hunt 1994), and our understanding of caste evolution remains incomplete. Queen-worker dimorphism has long been known to reflect strong influence of environmental factors, especially nutrition, in both bees (Michener, 1974) and ants (Hölldobler and Wilson, 1990). Wheeler (1986) suggests that an increase in the range of body sizes may have been a first step in queen-worker dimorphism among social Hymenoptera generally.

Among social wasps of the Vespidae, queen-worker dimorphism is apparently not found at all in the Stenogastrinae, whereas queen-worker dimorphism is typically pronounced in the Vespinae (but see Vecht, 1957; Matsuura and Yamane, 1984). Intermediate between these subfamilies is the Polistinae (Carpenter 1982), in which a range of conditions apparently exists from no caste dimorphism to discrete queen-worker dimorphism (Jeanne et al., 1995 and references therein). Among Polistinae, Epiponini is of interest as a taxon in which all species exhibit perennial coloniality and swarm-founding behavior (reviewed in Jeanne, 1991), arguably manifestations of social complexity, but queen-worker dimorphism has been reported as both present (e.g., *Protopolybia exigua*: Simões, 1977 in Jeanne et al., 1995) and absent (e.g., *Parachartergus colobopterus*: Strassmann et al., 1991). Jeanne et al. (1995) recently reported a detailed morphometric analysis of *Apoica pallens*, which is in the sister genus to the 21 other genera of Epiponini. They document a pattern of non-size-based queen-worker dimorphism that can

¹ This paper is dedicated to the memory of George C. Eickwort, colleague and friend.

only be explained by reprogramming of growth parameters (Wheeler, 1991) during the larval period. Occurrence of non-size-based caste difference in the basal genus of Epiponini calls for careful examination of other genera of Epiponini to ascertain the extent to which such caste difference may characterize the tribe. The work to be reported here was undertaken with this goal in mind.

Materials and Methods

Epipona is among the more derived of the 22 genera of Epiponini, the Neotropical swarm-founding polistine wasps (Wenzel and Carpenter, 1994). *Epipona guerini* (Saussure), one of 3 species in the genus, ranges from Mexico to Peru (Saussure, 1854; see J. M. Carpenter in prep. for clarification of species-level nomenclature of *Epipona*). A complete colony of *E. guerini* was collected at nightfall at Volcan Cacao Biological Station, Guanacaste Province, Costa Rica on 27 January, 1991. All adult wasps of the colony, freshly killed, were placed into 70% ethanol. Voucher specimens have been placed at the University of Missouri–St. Louis, INBIO (Heredia, Costa Rica), and the American Museum of Natural History.

Caste of females was determined by examination of the ovaries; queens were those with developed ova, and workers were those without. Fifty queens were prepared for morphometric analysis, as were fifty workers chosen haphazardly from more than twice that number dissected. Preparation consisted of pinning, removing the legs and wings from the left side of the body, and taping the removed forewing to a microscope slide. Measurements were then taken on 13 morphometric variables (Fig. 1) as defined and used by Jeanne et al. (1995): HH, head height; HW, head width; HL, head length; TH, thorax height; TW, thorax width; TL, thorax length; WL, wing length; G1BW, basal width of the first gastral tergite; G1AW, apical width of the first gastral tergite; G1H, first gastral tergite height; G1L, first gastral tergite length; G2W, second gastral tergite width; and G2L, second gastral tergite length. Measurements were taken using a zoom stereomicroscope equipped with a video camera linked to a computer programmed with DIAS, Digital Image Analyzer System (copyright 1993 The C. Squared Corporation). The system permitted continuous (vs. interval) measurement of all variables.

Data were common log transformed; all statistical analyses were performed using SAS (SAS version 6.02; SAS Institute, Cary, NC). Queen-worker difference for each variable was tested by independent *t*-tests. Stepwise discriminant analysis was used to identify the most significant contributors to caste difference. Stepwise regression analysis was then used to identify those variables that differed significantly in intercept between castes when regressed against thorax length. Analysis of covariance (ANCOVA) was used to test for homogeneity of slopes in queen vs. worker contrasts for those variables found to differ significantly by the stepwise regression.

Results

The colony contained an estimated 2675 adult wasps. A sample of 500 included 7 males (1.4%). Among females, queens and workers were unambiguously identifiable by the presence or absence of developed ova in the ovarioles. The colony contained approximately 60 queens (2.2%). Queens were larger than workers in all 13 morphometric variables (Table 1); all differences were significant by independent *t*-test at $P < 0.0001$. Stepwise discriminant analysis revealed three of

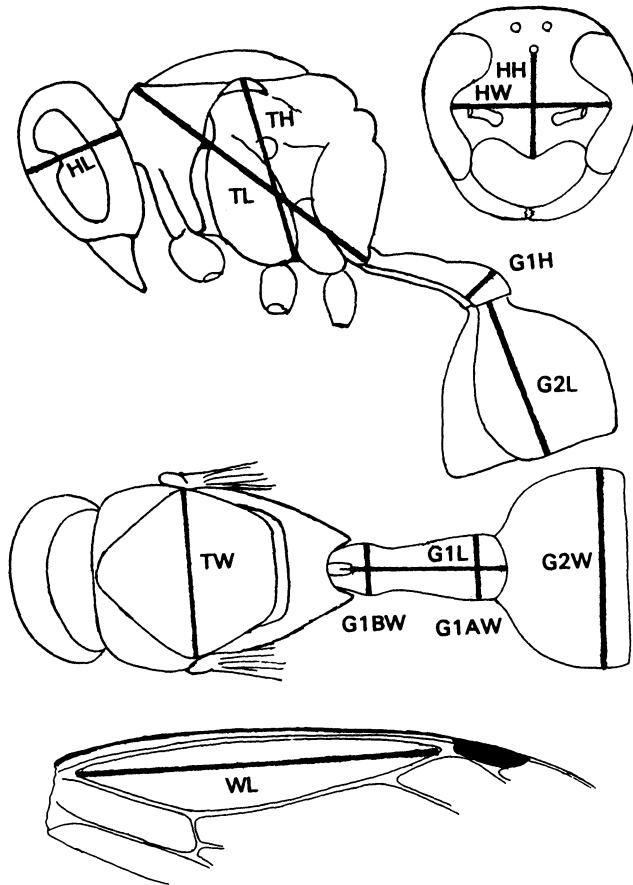


Fig. 1. Drawing of a female *Epipona guerini* to show the placement of the 13 morphometric variables (heavy straight lines); see text for names as labeled using abbreviations.

the 13 variables to be significant contributors to the total variance between queens and workers: thorax length (TL), width of the second gastral tergite (G2W), and height of the first gastral tergite (G1H). The greatest contribution to total variance between castes is attributable to thorax length. Accordingly, and in parallel with previous researchers (Jeanne and Fagen, 1974; Yamane et al., 1983; Kojima and Kojima, 1994; Jeanne et al., 1995), thorax length was used as the independent variable for queen vs. worker regression contrasts of the remaining variables. Stepwise regression showed that the major differences between queens and workers are determined by five variables (Table 2). These five variables were then tested independently using ANCOVA; queens and workers differ significantly in slope for G2W and WL with TL as covariate and caste as a fixed effect (Table 3, Fig. 2).

Discussion

Richards (1978) reported significant between-caste differences in *Epipona tatua* for number of hamuli, forewing length, and length (not width) of gastral tergite 1

Table 1. Means (mm) and standard deviations of 13 morphometric variables (see text) for queens ($n = 50$) and workers ($n = 50$) of *Epipona guerini*; Q/W = ratio of queen mean to worker mean.

Variable	Queens		Workers		Q/W
	Mean	SD	Mean	SD	
HH	1.24	0.06	1.16	0.08	1.07
HW	2.52	0.05	2.47	0.06	1.02
HL	1.54	0.08	1.48	0.08	1.04
TH	2.39	0.12	2.27	0.08	1.05
TW	2.27	0.06	2.12	0.09	1.07
TL	4.35	0.09	4.09	0.13	1.06
WL	5.52	0.10	5.29	0.21	1.04
G1H	0.73	0.04	0.66	0.05	1.12
G1BW	0.73	0.04	0.67	0.04	1.09
G1AW	0.99	0.05	0.90	0.04	1.10
G1L	2.31	0.15	2.20	0.13	1.05
G2W	3.28	0.10	3.04	0.11	1.08
G2L	2.63	0.08	2.22	0.11	1.18

(all $P < 0.001$). In the data for *E. guerini* reported here, queens are larger than workers for 13 morphometric variables. Nonetheless, perhaps due to overlap of the castes in all variables, caste dimorphism has not been previously reported in *E. guerini*. However, queens were readily identifiable during opening of the nest, as was independently observed in another colony of the same species (M. G. Keeping, pers. comm.). Difference in slopes of the regressions for two of the five significantly different variables but not for three others means that difference between the castes is not merely in size but also in body proportions: the slopes as well as intercepts of the allometries for G2W and WL differ between queens and workers, but those for TW, G1H and G1BW do not. The relationships for G2W plotted in Fig. 2A suggest diphasic allometry (see Wheeler, 1991, fig. 1B); the relationships for WL plotted in Fig. 2B suggest complete dimorphism (Wheeler, 1991, fig. 1D).

The queens in *E. guerini* seem potential exemplars of a previously held view that caste in epiponine wasps is primarily size based (Jeanne et al., 1995; see also Jeanne and Fagen, 1974; see Yamane et al., 1983; Kojima and Kojima, 1994; and Wenzel, 1992 for examples from *Ropalidiini*). In the terminology of Wheeler (1991), size-based difference in caste reflects reprogramming during larval growth of critical size for metamorphosis. However, the combination of continuously variable measurements and multivariate analysis has revealed two contrasts in which

Table 2. Stepwise regression of queen-worker dimorphism in *Epipona guerini* based on 13 morphometric variables, using TL (thorax length) as the independent variable and all others as dependent variables. Five variables, tabulated here, contribute significantly to queen-worker discrimination.

Step	Variable	Partial R^2	Model R^2	F	$P > F$
1	TW	0.5598	0.5598	124.6	0.0001
2	G2W	0.0807	0.6047	21.7	0.0001
3	WL	0.0424	0.6828	12.8	0.0005
4	G1H	0.0178	0.7007	5.6	0.0194
5	G1BW	0.0169	0.7176	5.6	0.0196

Table 3. *F* values for analyses of covariance (ANCOVA) of five morphometric variables (see text) with thorax length (TL) as the covariate and caste (queen or worker) as a fixed effect. For all, d.f. = 1, 96. Significance levels: *** = <0.001; ** = <0.01; * = <0.05.

Dependent variable	<i>F</i> values		
	TL	caste	TL-Caste
TW	134.88***	9.67**	0.41
G2W	138.46***	27.06***	6.10*
WL	87.98***	1.81	5.86*
G1H	71.60***	9.05**	0.06
G1BW	90.32***	0.36	1.87

caste difference cannot be explained by a single size-based allometric relationship that contains both castes. The differences in G2W and WL reflect reprogramming during larval growth of growth parameters (Wheeler 1991). The reprogramming of growth parameters during larval growth found in *Apoica pallens* by Jeanne et al. (1995) does not incorporate overall size difference as in the present case.

Using the terminology of Kukuk (1994), both *A. pallens* and *E. guerini* are “morphologically, permanently eusocial” species. Since *Apoica* and *Epipona* represent both basal and derived genera of Epiponini (Wenzel and Carpenter, 1994), the question now arises whether non-size-based queen-worker dimorphism and pre-imaginal caste determination are characteristic of them all. Pre-imaginal queen-worker dimorphism has been previously reported for *Agelaia* (Jeanne and Fagen, 1974; Simões, 1977 in Jeanne et al., 1995), *Protopolybia exigua* (Simões, 1977 in Jeanne et al., 1995), *Protopolybia acutiscutis* (Richards and Richards, 1951), *Polybia occidentalis* (Richards and Richards, 1951), and *Polybia bistrriata* (Richards and Richards 1951); pre-imaginal dimorphism has recently been reported for *Pseudopolybia difficilis* (Jeanne, 1996). Numerous other morphometric and color differences between queens and workers of Epiponini are given by Richards (1978; see especially Table 2). Queen-worker dimorphism has been reported to be absent in *Parachartergus colobopterus* (Strassmann et al., 1991), but that analysis includes measurements of neither the thorax nor gaster, both long known to be important in wasp caste differentiation (Jeanne and Fagen 1974). Very small (e.g., *Leipomeles*) and large (e.g., *Synoeca*) wasps could especially enlighten a survey of caste dimorphism in Epiponini, but small colonies of many species may cause problems of adequate sample size for rigorous statistical analysis.

The occurrence of non-allometric pre-imaginal caste determination in basal and derived genera of Epiponini suggests generality of the phenomenon and possible origin before the derivation of Epiponini. Very strong evidence now exists for nutritionally influenced pre-imaginal “bias” in queen vs. worker roles in the independent-founding *Ropalidia marginata* (Gadagkar et al., 1988, 1990, 1991), and Grechka (1986) reports pre-imaginal caste determination in *Polistes dominulus* (as *P. gallicus*). Grechka (1986) and Hunt (1991, 1994) argue a focal role for variable nourishment in caste determination in *Polistes*. The link between variable nourishment, caste, and possible subtle differences in queen vs. worker allometries in *Polistes* merit aggressive investigation. So, too, should we focus on the physiology of pre-imaginal caste determination and its underlying molecular basis in social Hymenoptera generally.

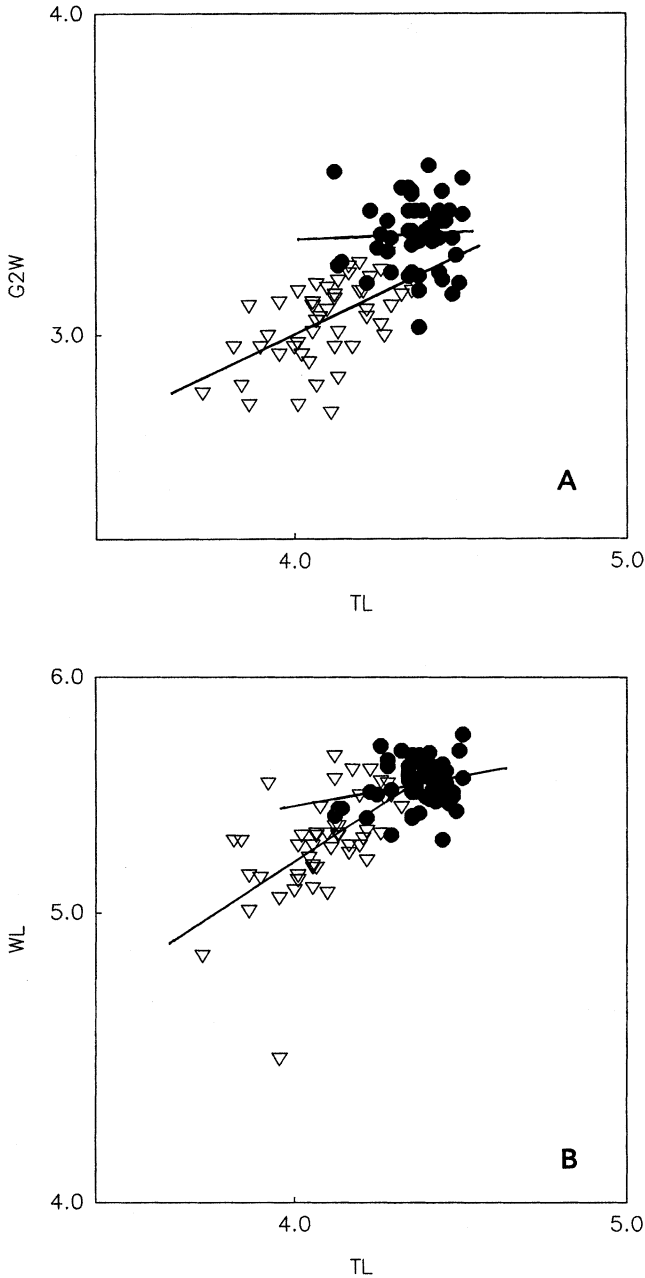


Fig. 2. Log-log plots of G2W (A, upper) and WL (B, lower) versus TL. Filled circles = queens; hollow triangles = workers.

Acknowledgments

Research was supported by NSF grants BSR-8805971 and DIR-91-03255 and by a Research Award from the University of Missouri–St. Louis. Logistics support was provided by Organization for Tropical Studies course 91-1, for which B. A.

Loiselle merits special thanks. T. C. Bukowski helped to collect the wasp colony and was stung for his troubles. J. M. Carpenter determined the species identity and provided a helpful review of the manuscript. J. G. Blake made the microscope and computer system available for our use, and G. Servat helped us learn how to use it. D. E. Wheeler gave thoughtful feedback on a draft of the manuscript, as did two anonymous reviewers. R. L. Jeanne merits special thanks for helping shape the project and for providing continuous suggestions and a careful review of the manuscript.

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