Naturwissenschaften 82, 296–298 (1995) © Springer-Verlag 1995

Non-Size-Based Morphological Castes in a Social Insect

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The division of colonies into castes, each composed of individuals performing the same specialized set of tasks, lies at the heart of social organization in the insects and is one of the defining criteria of eusociality [1–3]. While in some eusocial insects the queen and worker castes differ only in behavior, in others the behavioral differences are accompanied by size and morphological specializations [4]. Queen and worker castes that are morphologically distinct are widespread in all three groups of eusocial Hymenoptera (ants, bees, and wasps). Worker polymorphism, or the existence of two or more morphologically specialized worker subcastes, is restricted to 15% of the ant genera, where it has had eight independent evolutionary origins [5]. In both cases, differential treatment of the immature stages, typically in the form of nutritional differences, triggers switches leading to two or more developmental programs [6].

Evidence from comparative morphometric studies suggests that the first step in the evolution of worker subcastes in ants was an increase in the size range of workers. This served as a substrate for the second step, the evolution of allometry-based morphological differences among workers along the size gradient [6]. With respect to the evolutionary divergence of queens and workers, the evidence is less clear, but suggests that the initial step was also an expansion of the range of female body size [7].

We provide the first evidence that morphological castes may evolve without an initial divergence in body size. Queens and workers in a polistine wasp differ significantly in body proportions while differing little in overall size. We argue that in at least some eusocial Hymenoptera, morphologically specialized queen and worker castes are not derived from allometric growth along a body-size gradient, unlike physical subcastes in worker ants.

Apoica belongs to a tribe of 22 genera of swarm-founding wasps (Hymenoptera:

Table 1. Summary statistics of morphometrics on queens and workers of *Apoica pallens* (in mm). Q/W is the ratio of the means of queens and workers. *P* value gives level of significance of independent t-test. $N = 50$ queens, 50 workers. HH (head height) = tip of clypeus to ventral rim of median ocellus (frontal aspect); HW (head width) = maximum interorbital distance (frontal aspect); HL (head length) = rear margin gena to front of compound eye, with longitudinal axis horizontal (lateral aspect); TH (thorax height) = height of mesothorax from dorsal end of mesopleural suture to most ventral projection of mesopleuron (lateral aspect); TW (thorax width) = greatest width of mesoscutum (dorsal aspect); TL (thorax length) = from anterior projection of pronotal keel to rear margin of propodeal valve (lateral aspect); WL (wing length) = maximum length of the radial cell of the forewing; G1AW (first gastral tergite apical width) = width at apical margin of gastral tergite 1 (petiole) (dorsal aspect); G1BW (first gastral tergite basal width) = minimum width of the base of gastral tergite 1 (dorsal aspect); G1H (first gastral tergite height) = maximum height of gastral tergite 1 (lateral aspect); G1L (first gastral tergite length) = length of gastral tergite 1 from muscle insertion to apical margin (dorsal aspect); G2W (second gastral tergite width) = maximum width of gastral tergite 2 (dorsal aspect); G2L (second gastral tergite length) = length of gastral tergite 2, from posterior-most projection of gastral tergite 1 to apical margin of gastral tergite 2 (lateral aspect)

Measure	Queens		Workers		Q/W	*P*<
	Mean	(SD)	Mean	(SD)		
HH	2.45	(±0.04)	2.58	(±0.05)	0.95	0.001
HW	2.66	(±0.06)	2.86	(±0.07)	0.93	0.001
HL	0.40	(±0.01)	0.42	(±0.01)	0.94	0.001
TH	2.41	(±0.06)	2.47	(±0.08)	0.98	0.001
TW	2.28	(±0.06)	2.25	(±0.07)	1.01	0.050
TL	5.51	(±0.14)	5.63	(±0.14)	0.98	0.001
WL	9.11	(±0.26)	9.66	(±0.27)	0.94	0.001
G1H	0.22	(±0.01)	0.21	(±0.01)	1.03	0.002
G1AW	0.41	(±0.01)	0.37	(±0.01)	1.11	0.001
G1BW	0.14	(±0.01)	0.13	(±0.01)	1.01	0.070
G1L	3.37	(±0.11)	3.60	(±0.07)	0.94	0.001
G2W	3.10	(±0.21)	2.86	(±0.18)	1.08	0.001
G2L	3.00	(±0.17)	3.30	(±0.14)	0.91	0.001

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Vespidae: Polistinae: Epiponini) found in the tropics. The tribe exhibits the full range of degrees of caste differentiation, from species in which queens and workers are apparently identical in size to those with castes that are discontinuous in size and morphology [8]. *Apoica,* the sister genus to the remaining 21 tribal genera [9], is unusual in that queens are slightly smaller than workers [10]. The Epiponini are polygynous, meaning that their colonies contain multiple egg-laying queens [8].

We collected a colony of *A.pallens* (F.) in October 1993 in the state of Cojedes, Venezuela. A random sample of the 499 adult females was later dissected and separated into two categories on the basis of ovary development. Females with at least one partially yolked egg per ovariole were classified as queens, and those with filamentous ovarioles as workers. Females were sorted unambiguously by this criterion; there were no individuals with intermediate ovary development. Spermathecae were not examined. Fifty queens and 50 workers were randomly selected from the dissected sample and were measured with respect to 13 morphometric variables (Table 1). All analyses were made using common log transformations of the raw data.

Queens and workers differed little in overall size; the queen/worker size ratio for the 13 characters averaged only 0.98. However, queens tended to be significantly smaller than workers anteriorly, but significantly larger posteriorly (Table 1). Analysis of covariance [11] supported models of each variable vs. thorax length (chosen as a measure of body size) that had significantly different linear relationships for queens and workers. For all measurements there was strong evidence that the lines for queens and workers were either parallel to one another or had a common intercept at 0 ($P<0.02$). Large variance combined with a small size range precluded distinguishing between these two models. For three variables (G1H, G1AW, G2W) the null hypothesis that the slope did not differ from 0 could not be rejected.

Stepwise discriminant analysis identified head width (HW) and first gastral tergite apical width (G1AW) as the two most important contributors to the separation of the castes, together accounting for 85% of the variation. Plotting each of these against thorax length clearly shows that simple allometric growth cannot explain the two castes (Fig. 1). Plotting G1AW against HW illustrates the discreteness of the castes as well as the anterior-posterior change in relative body proportions (Fig. 2). The clean separation of individuals into two morphologically distinct groups on the basis of ovary development makes us confident that our criterion for separating queens from workers was valid.

The existence of significant shape differences in the presence of only a minor overall size difference strongly suggests that the two castes could not have diverged along a gradient of body size: there is no way to move from one caste to the other simply by changing size. Thus, the morphological difference cannot be accounted for by simple linear allometric growth. This leads us to hypothesize that the first evolutionary step in the divergence of queens and workers in these wasps, and perhaps other social Hymenoptera, was a reprogramming of growth parameters in the pre-adult stage rather than an expansion of the range of body size, such as underlies worker polymorphism in ants [6].

Our result points to the possibility that some of the epiponine species, thought to lack morphological castes on the grounds that queens and workers do not differ significantly in size [8], may actually be

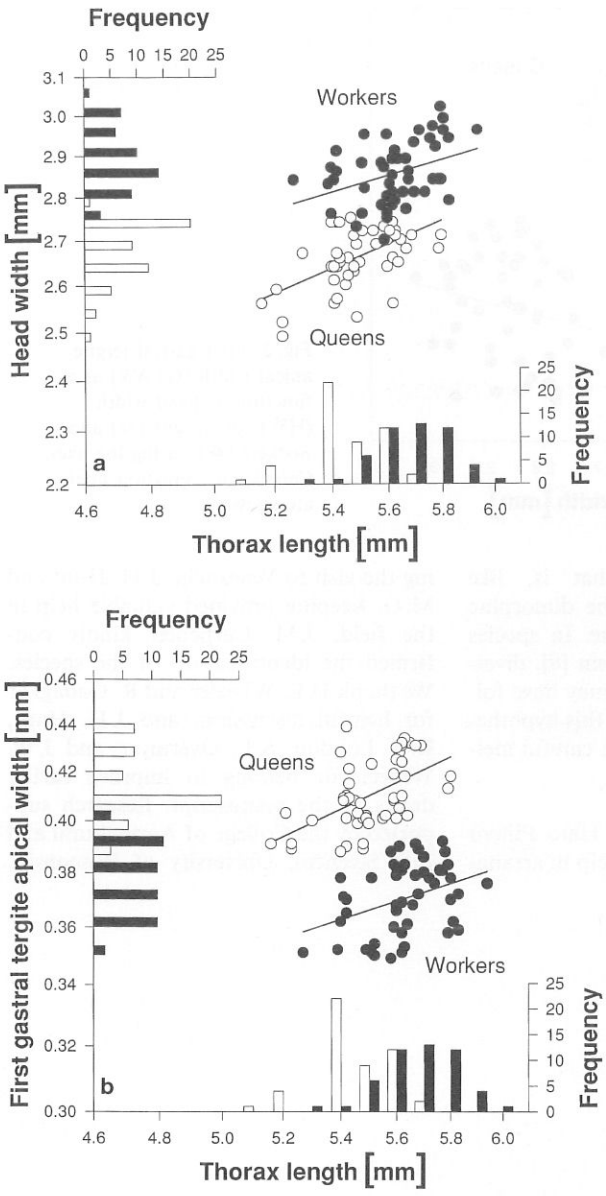

Fig. 1. a) Head width (HW) and b) first gastral tergite apical width (G1AW) as functions of thorax length (TL) for queens (○) and workers (●) on log-log axes. Calculated regression lines are shown. Also plotted are frequency distributions of each caste on each variable (each *pair of bars* is centered on the tick, which indicates the upper limit of the interval represented)

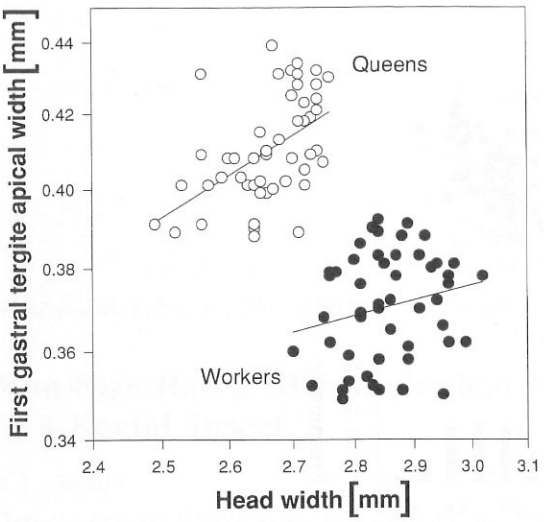

Fig. 2. First gastral tergite apical width (G1AW) as a function of head width (HW) for queens (○) and workers (●) on log-log axes. Calculated regression lines are shown

'cryptically dimorphic'; that is, like *Apoica pallens,* they may be dimorphic on the basis of shape alone. In species with a strong size dimorphism [8], divergence along a size gradient may have followed secondarily, although this hypothesis remains to be tested with careful metric studies.

Our thanks to the staff of Hato Piñero and to Dr. K. Jaffe for his help in arranging the visit to Venezuela. J. H. Hunt and M. G. Keeping provided valuable help in the field. J. M. Carpenter kindly confirmed the identification of the species. We thank D. E. Wheeler and R. Gadagkar for helpful discussion, and J. H. Hunt, K. B. London, S. L. Overmyer, and J. W. Wenzel for helping to improve earlier drafts of the manuscript. Research supported by the College of Agricultural and Life Sciences, University of Wisconsin, Madison, and by US National Science Foundation grant no. IBN-9222108 to RLJ.

Received January 9 and March 20, 1995

1. Wilson, E. O.: The Insect Societies. Cambridge, MA: Harvard Univ. Press 1971
2. Sherman, P. W., et al.: Behav. Ecol. *6*, 102 (1995)
3. Crespi, B. J., Yanega, D.: ibid. *6*, 109 (1995)
4. Oster, G. F., Wilson, E. O.: Caste and Ecology in the Social Insects. Princeton, NJ: Princeton Univ. Press 1978
5. Hölldobler, B., Wilson, E. O.: The Ants. Cambridge, MA: Harvard Univ. Press 1990
6. Wheeler, D. E.: Am. Nat. *138*, 1218 (1991)
7. Wheeler, D. E.: ibid. *128*, 13 (1986)
8. Jeanne, R. L., in: The Social Biology of Wasps (K. G. Ross, R. W. Matthews, eds.). Ithaca, NY: Cornell Univ. Press 1991
9. Carpenter, J. M., in: ibid.
10. Richards, O. W.: The Social Wasps of the Americas Excluding the Vespinae. London: British Museum (Natural History) 1978
11. Littell, R. C., et al.: SAS System for Linear Models. Cary, NC: SAS Institute Inc. 1991

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