Novitates

Evolution of Caste in Neotropical Swarm-Founding Wasps (Hymenoptera: Vespidae; Epiponini)

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ABSTRACT

Reproductive castes are compared in species of swarming wasps representing all currently recognized genera of Epiponini (Polistinae). New morphometric data for nine measures of body parts and ovarian data are presented for 13 species. These are integrated with all similarly conducted available studies, giving a total of 30 species. Analysis reveals several syndromes relating reproductive and nonreproductive individuals: no meaningful distinction, physiological differences only, reproductives larger than nonreproductives with intermediate individuals present, reproductives different in shape from nonreproductives with no intermediates, and reproductives smaller in some aspects than nonreproductives. Distribution of these syndromes among species is consistent with phylogenetic relationships derived from other data. Optimizing these syndromes on the cladogram indicates that the basal condition of Epiponini is a casteless society that is not comparable to the primitively social genus *Polistes* where dominant queens control reproduction. Castes originate several times in Epiponini, with different results in different lineages. The best documented evolutionary sequence passes from casteless societies, to those with reproductives larger, to those with reproductives differing in shape from nonreproductives, to those with reproductives smaller in some measures. This sequence is consistent with Wheeler's theory of the origin of caste through developmental switches, and represents the most thorough test of that theory to date.

INTRODUCTION

Separation into castes is one of the cornerstones of the evolution of social insects.

In some species, reproductive "queens" and nonreproductive "workers" differ only in behavior, but in other species such behaviors are accompanied by physiological and mor-

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phological specializations and body-size variation (Oster and Wilson, 1978). The degree to which castes are distinct often serves as part of the definition of the society itself, with greater caste differentiation indicating ''higher'' sociality (Bourke, 1999). In some groups, such as swarm-founding neotropical wasps, the species are described as highly social, although the distinction between queens and workers is considered slight and often confusing (Richards and Richards, 1951; Richards, 1978, cited as Polybiini, junior synonym of Epiponini, see Carpenter, 1993, 1997).

Wasps (Hymenoptera: Vespidae) have frequently been used to test evolutionary models for the origin of social behavior because of their different levels of sociality—from solitary to eusocial (West-Eberhard, 1978, 1996; Wilson, 1985; Itô, 1986; Spradbery, 1991). General theory holds that primitive systems of dominance rely on physical aggression, with the winner becoming the egglayer. More derived systems require some kind of caste determination that may occur during the immature stages of an individual's development (preimaginal determination), with an unambiguous physiological or morphological result that cannot be reversed. Absence of morphological castes is a plesiomorphic (''primitive'') condition in the three subfamilies of social wasps, so that morphological castes were attained independently in different lineages (Carpenter, 1991). Most distant to the question at hand, females of Stenogastrinae are barely distinguished as queens or as workers (Turillazzi, 1991). Closer, and sister to the subfamily examined here, queens of Vespinae are larger than workers (Spradbery, 1991), but such a trait may be an adaptation for a queen's solitary winter survival in most species (West-Eberhard, 1978). In the Polistinae (studied here), the most basal genera (*Polistes* and *Mischocyttarus*), initiate their nests solitarily, with egglayers only slightly larger than non-egglayers. However, polistines present a large

diversity that can be arranged along a spectrum from taxa in which queens and workers are externally similar, to others with fairly distinct caste attributes (reviewed in O'Donnell, 1998; Shima et al., 1998). The Paleotropical tribe Ropalidini (perhaps the sister to the Neotropical tribe Epiponini examined here) shows diversity that is hard to interpret without more study. For instance, some species of *Ropalidia* present distinct morphological castes (Yamane et al., 1983), including those of small colony size (Wenzel, 1992), but others show morphologically similar castes despite larger colony size (Gadagkar and Joshi, 1982, 1983; Yamane and Itô, 1987; Gadagkar, 1987). *Parapolybia* has castes (Yamane and Maeta, 1985) but their behavior is poorly known. *Belonogaster* is also poorly known (Pardi and Piccioli, 1981) but is thought to show great morphological variation (Keeping, 2000, 2002). In *Polybioides*, morphological castes are known in *P. tabidus* (Turillazzi et al., 1994), which builds large colonies and reproduces by swarms. However, despite the repeated evolution of castes in social wasps as a whole, the evolution of castes is largely interpreted through our understanding of Epiponini.

Epiponini is a tribe of Polistinae, with about 20 well-marked genera and at least 229 species, plus another 27 subspecies, all of which are Neotropical. All Epiponini are polygynic (meaning that many queens commonly reproduce simultaneously on the same nest), and all reproduce by swarms, which is taken as a sign of sophisticated, obligatory, high sociality. Initially, Richards (1978) documented three forms of caste discrimination, and recent research builds upon these: (1) Queens larger than workers. In some species caste differences are so pronounced that they must be determined by nutritional differences during larval development (Evans and West-Eberhard, 1970; Jeanne and Fagen, 1974; Sakagami et al., 1996; Noll et al., 1997), with important consequences for fertility and reproductive asymmetries (West-Eberhard,

1978; O'Donnell, 1998). The classical land-mark is a case of different, nonallometric castes of *Agelaia areata*, where queens and workers have different shapes as well as different sizes (Jeanne and Fagen, 1974). It seems that these differences must represent preimaginal bias in nutrition. (2) Allometric differences, with queens smaller than workers in some body parts, but larger in others, which may result from ontogenetic reprogramming in growth parameters (Jeanne et al., 1995), according to the idea that the body plans represent fundamentally different end products, not different points along a continuum. Sometimes such castes are barely detectable (Jeanne, 1996). (3) Slight or indistinct morphological differences, with castes absent, or manifested weakly, based on only a few traits (Richards, 1978; Jeanne, 1980). One great problem is that integration of the empirical studies is not straightforward because few studies are exactly comparable in measurement methodology or phase of colony cycle studied, so generalization is difficult. A rough summary of species known to fall into these three conditions can be found in table 1. It has been suggested that preimaginal determination may be basal for Epiponini (Jeanne et al., 1995; Jeanne, 1996; Hunt et al., 1996; O'Donnell, 1998), especially because such a trait is present in *Apoica* (Shima et al., 1994), the most basal genus in Epiponini. However, *Apoica* is peculiar and highly apomorphic in many ways (general morphology, nest architecture, and nocturnal habit, see Richards, 1978; Wenzel, 1992; and Pickett, 2003) and so it may not be a good model of basal synapomorphies of Epiponini. It has not been demonstrated that preimaginal determination is the basal condition for the whole clade.

Integrating studies of caste in Epiponini is difficult because studies to date have been limited in scope, with most publications covering one species at a time. Measurements are not necessarily comparable across studies. There are sometimes doubts about the

TABLE 1
Morphometric Differences Reported from Literature

No Significant Differences:

Angiopolybia pallens[12,15], *Asteloeca traili*[12], *Brachygastra lecheguana*[25], *B. moebiana*[15], *Chartergellus communis*[15,17], *Clypearia sulcata*[12], *M. cingulata*[13,14], *Parachartergus smithii*[8], *Pa. colobopterus*[26], *Pa. fraternus*[15,21], *Polybia bicytarella*[13], *Po. chrysothorax*[15], *Po. erythrothorax*[15], *Po. micans*[15], *Po. quadricincta*[15], *Synoeca chalibea*[15], *S. surinama*[12,15], *Pseudopolybia vespiceps*[24]

Queens Larger:

Agelaia areata[6], *A. fulvofasciata*[15], *A. lobipleura*[15], *A. yepocapa*[5], *Brachygastra augusti*[3,a], *B. bilineolata*[15], *Charterginus fulvus*[12], *Chartergus chartarius*[15], *C. globiventris*[10], *C. metanotalis*[12], *Epipona tatua*[12,15], *E. guerini*[4], *Leipomeles dorsata*[12], *Metapolybia docilis*[2], *Nectarinella championi*[12], *Polybia belemensis*[15], *Po. bistriata*[13,b], *Po. catillifex*[13,c], *Po. emaciata*[15], *Po. jurinei*[15], *Po. occidentalis*[15,19], *Po. platycephala*, *Po. sylvestris*[13], *Po. rejecta*[12,15], *Po. ruficeps*[15], *Po. scutellaris*[15,18], *Po. singularis*[15], *Po. spinifex*[12], *Po. striata*[15], *Protonectarina sylveirae*[23], *Protopolybia exigua*[10], *Pr. minutissima*[13], *Pr. pumila*[13], *Pr. sedula*[15], *Pseudopolybia compressa*[15], *Synoeca cyanea*[9]

Queens Smaller in Some Measures, Larger in Others:

Agelaia multipicta[11], *Ag. pallipes*[15,11], *Ag. vicina*[1], *Apoica flavissima*[22], *Ap. gelida*[15], *Ap. pallens*[15,16], *Brachygastra scutellaris*[13,14], *Metapolybia aztecoides*[12], *Polybia dimidiata*[15,20], *Po. liliacea*[12], *Pseudopolybia difficilis*[7]

Index to References:

a Richards (1978) found no differences.
b Carpenter and Ross (1984) found queens slightly smaller than workers, but not significantly different.
c Richards and Richards (1951) found no differences.

1 Baio et al. (1998)	14 Carpenter and Ross (1984)
2 Baio et al. (2003a)	
3 Baio et al. (2003b)	15 Richards (1978)
4 Hunt et al. (1996)	16 Jeanne et al. (1995)
5 Hunt et al. (2001)	17 Mateus et al. (1999)
6 Jeanne and Fagen (1974)	18 Noll and Zucchi (2000)
7 Jeanne (1996)	19 Noll et al. (2000)
8 Mateus et al. (1997)	20 Shima et al. (1996b)
9 Noda et al. (2003)	21 Mateus et al. (2004)
10 Noll and Zucchi (2002)	22 Shima et al. (1994)
11 Noll et al. (1997)	23 Shima et al. (1996a)
12 Present data	24 Shima et al. (1998)
13 Richards and Richards (1951)	25 Shima et al. (2000)
	26 Strassmann et al. (1991)

phase of colony cycle that was measured, particularly when the colony was collected opportunistically by visitors on brief field-trips. In addition, when reproductive status does not relate closely to morphological variation, there is a tendency to rescue a concept of caste by categorizing problematic females as ''laying workers'' or ''replacement queens'' on an ad hoc basis. Such axiomatic descriptions may serve only to obscure the original question, protecting an inadequate concept of caste itself from refutation by empirical data. We address these issues by presenting here the most complete set of comparable values regarding caste determination. A total of more than 13,500 measures encompassing nine dimensions of 13 species are offered for the first time. These are integrated with comparable data from other studies to include 68 species. We establish the basal condition for Epiponini, providing evidence for both preimaginal and postimaginal caste determination. In addition to morphometric variation in caste, we stress the existence of various types of social regulation.

MATERIALS AND METHODS

Workers and queens were taken from mature colonies (i.e., post worker emergence) of 13 different species of Epiponini collected in three different localities. *Angiopolybia pallens* (Lepeletier), *Asteloeca ujhelyii* (Ducke), *Charterginus fulvus* Fox, *Clypearia sulcata* (de Saussure), and *Leipomeles dorsata* (Fabricius) were collected in Iquitos, Peru. *Nectarinella championi* (Dover) was collected in Costa Rica, near Atenas. For these two localities, the samples were collected by John W. Wenzel and James Carpenter, killed in cyanide and preserved promptly in 70% ethanol, and deposited in the AMNH. *Polybia* (*Polybia*) *liliacea* (Fabricius), *Polybia* (*Formicicola*) *rejecta* (Fabricius), *Chartergus metanotalis* Richards, *Epipona tatua* (Cuvier), *Metapolybia aztecoides* Richards, *Polybia* (*Pedothoeca*) *spinifex* Richards, and *Synoeca surinama* (Linnaeus) were collected in Nova Xavantina, Mato Grosso, Brazil by Fernando B. Noll and Sidnei Mateus. Vouchers are deposited at the Museu de Zoologia (MZUSP),

São Paulo, Brazil, and the AMNH. They were taken by being put into a plastic bag provided with ether-moistened cotton balls or with open cyanide tubes. Populations were fixed in Dietrich's solution and then kept in 70% ethanol for dissection.

From each of these colonies 100 workers and all queens were measured and dissected. When castes could be discriminated by size or color, all possible queens were selected, and from the remaining individuals 100 workers were arbitrarily selected. In small colonies where castes were not obvious, all individuals were measured and dissected. In large colonies where castes were hard to identify, 100 individuals were chosen randomly. After identifying some morphological characters to discriminate queens, such as abdominal size, all individuals having such a pattern were chosen and used in the analysis. The following characters were measured under a binocular microscope (smallest unit = 0.01 mm): head width (HW), minimum interorbital distance (IDm), gena width (GW), width of mesoscutum (MSW), alitrunk length (AL), length of gastral tergite I (T_1L), basal height of T_1 (T_1BH), basal widths of tergite II (T_2BW), and partial length of the forewing (WL) (fig. 1, for more details about the characters see Shima et al., 1994). Ovary condition was determined 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 ethanol (70%). The presence of sperm cells was confirmed by microscope.

Before statistical analysis, data were converted to millimeters and later converted by log transformation in order to avoid problems of variance. Means and standard deviations were calculated from the nine morphological measurements. Statistical characterization of caste was explored in two ways. One-way ANOVA was used for comparisons of means to demonstrate whether castes (as determined by dissection) differ in some body dimensions. Because multiple measures that relate to shape are not always captured well in single comparisons, stepwise discriminant function analysis was used to see if combinations of variables could be useful in predicting caste. In this method, variables are successively added to the model based on the
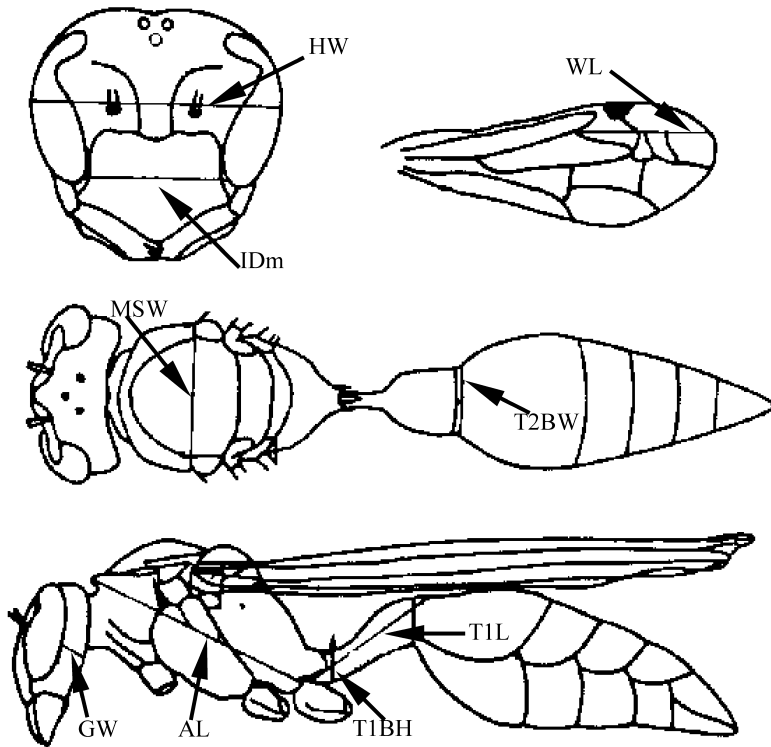
Fig. 1. Representative measures for morphometric analyses of this paper: head width (HW), minimum interorbital distance (IDm), gena width (GW), width of mesoscutum (MSW), alitrunk length (AL), length of gastral tergite I (T_1L), basal height of T_1 (T_1BH), basal widths of tergite II (T_2BW), and partial length of the forewing (WL).

higher *F to enter* values, adding no more variables when the *F*-ratio is no longer significant. However, variables that enter the model early may be completely subsumed by separate variables that enter later. The significance of Wilks' lambda (an estimate of common variance between sets of variates) was used to determine the degree to which separate measures contributed to the final model. This is an alternative to using an *F to remove* at each step. Variables that appear in the 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 the discrimination itself. Wilks' lambda varies from zero to one: the lower the value, the greater the significance.

Analysis of covariance (ANCOVA) was used, with alitrunk length (AL) as a covariate, in order to identify different growth rates in the body parts measured. AL was chosen based on the effectiveness in previous publications (Jeanne et al., 1995; Jeanne, 1996; Hunt et al., 1996).

RESULTS

OVARIAN DEVELOPMENT

The ovariole number was always three in each ovary, and the following types of ovarian development were distinguished (table 2); type A: with filamentous ovarioles that had no visible oocytes or with some very small oocytes; type B: bearing some young oocytes; type C: with one or more mature oocytes in each ovariole; type D: with well-developed and very long ovarioles coiled inside the gaster, with at least one mature egg. Only females with type D ovaries were inseminated. All four types were found in the following species: *Angiopolybia pallens*, *Charterginus fulvus*, *Leipomeles dorsata*, and *Nectarinella championi* (table 2). Type

TABLE 2
Ovary Development for All Species Analyzed[a]

	N	Ovaries (%)			
	females	A	B	C	D
Angiopolybia pallens	500	21	7	54	28
Asteloeca ujhelyii	18	22	28		50
Charterginus fulvus	29			79.3	20.7
Chartergus metanotalis	812	67	24		9
Clypearia sulcata	138	73.6	25		1.4
Epipona tatua	6,752	66.5	33		0.5
Leipomeles dorsata	105	41	31	15	12
Metapolybia aztecoides	251	59	27		14
Nectarinella championi	98	41	21	29	11
Polybia liliacea	22,384	66.6	33		0.4
Polybia rejecta	3,838	60	38		2
Polybia spinifex	997	43.9	55		1.1
Synoeca surinama	1,478	48	45		7

[a]See text for explanation.

C was not found in *Asteloeca ujhelyii, Chartergus metanotalis, Occipitalia sulcata, Epipona tatua, Metapolybia aztecoides, Polybia liliacea, Polybia rejecta, Polybia spinifex,* and *Synoeca surinama* (table 2). Queens' ovaries (type D, inseminated) were much longer than workers' ovaries in *Chartergus metanotalis, Epipona tatua, Polybia liliacea, Polybia rejecta,* and *Polybia spinifex.* No species of this study lacked both types B and C.

MORPHOLOGICAL DIFFERENCES

Differences of mean values of nine characters measured were tested in workers and queens (tables 3–6). Univariate statistics (ANOVA) showed that measured characters could be different or not between queens and workers in different species. Also, based on multivariate statistics, the power of discrimination of each measurement varied in the different species studied; that is, the measurements may discriminate castes independently or only in combination.

In a first group (fig. 2), morphological differences between castes were totally or practically absent in the following species: *Angiopolybia pallens, Asteloeca ujhelyii, Clypearia sulcata* (table 3), *Leipomeles dorsata, Metapolybia aztecoides, Nectarinella championi,* and *Synoeca surinama* (table 4). ANOVA showed no significant differences in any measurement in *An. pallens, As. ujhelyii,* and *Cl. sulcata;* in *S. surinama,* only one measurement was significant, and in *L. dorsata, M. aztecoides,* and *N. championi* three measurements were significant. Except for *M. aztecoides,* in which some characters were smaller in queens than in workers, differences were always based on queens being larger than workers. ANCOVA, using alitrunk length as a dependent variable (table 7), was not significant in any character in *An. pallens, As. ujhelyii,* and *Cl. sulcata.* In *L. dorsata, M. aztecoides, N. championi,* and *S. surinama,* significant differences were detected.

Wilks' lambda values were used to infer the independent contribution of each variable

TABLE 3
Means and Observed Values of ANOVA Test, for Nine Characters Used for Discriminating Castes of
Angiopolybia pallens, Asteloeca ujhelyii, **and** *Clypearia sulcata*

	Angiopolybia pallens			*Asteloeca ujhelyii*			*Clypearia sulcata*		
	Queens (N = 18)	Workers (N = 82)	ANOVA (F)	Queens (N = 9)	Workers (N = 9)	ANOVA (F)	Queens (N = 10)	Workers (N = 115)	ANOVA (F)
HW	4.49 ± 0.05	4.44 ± 0.45	0.28	3.34 ± 0.07	3.35 ± 0.10	0.01	3.06 ± 0.03	3.02 ± 0.07	0.75
IDm	0.77 ± 0.06	0.76 ± 0.06	0.40	1.63 ± 0.05	1.63 ± 0.05	0.01	1.25 ± 0.03	1.25 ± 0.03	0.03
GW	1.87 ± 0.03	1.86 ± 0.04	0.19	0.98 ± 0.05	0.97 ± 0.07	0.01	0.53 ± 0.03	0.53 ± 0.02	1.93
MSW	2.82 ± 0.06	2.82 ± 0.07	0.01	1.99 ± 0.09	2.07 ± 0.15	2.05	1.86 ± 0.03	2.00 ± 0.18	1.12
AL	6.02 ± 0.15	5.97 ± 0.18	1.22	4.59 ± 0.21	4.52 ± 0.18	2.08	4.27 ± 0.12	4.00 ± 0.20	3.79
T_1L	3.65 ± 0.14	3.65 ± 0.19	0.01	2.56 ± 0.10	2.51 ± 0.11	2.91	2.28 ± 0.15	2.15 ± 0.13	1.87
T_1BH	0.67 ± 0.03	0.68 ± 0.04	0.67	0.51 ± 0.03	0.49 ± 0.05	0.83	0.32 ± 0.01	0.34 ± 0.04	0.30
T_2BW	1.69 ± 0.07	1.70 ± 0.07	0.04	0.95 ± 0.06	0.99 ± 0.10	0.93	1.13 ± 0.02	1.22 ± 0.15	0.76
WL	6.65 ± 0.14	6.64 ± 0.12	0.14	4.64 ± 0.41	4.77 ± 0.18	0.72	3.34 ± 0.08	3.30 ± 0.12	0.16

No differences are significant at $p < 0.05$.

TABLE 4
Means and Observed Values of ANOVA Test, for Nine Characters Used for Discriminating Castes of
Leipomeles dorsata, Metapolybia aztecoides, Nectarinella championi, **and** *Synoeca surinama*

| | *Leipomeles dorsata* | | | *Metapolybia aztecoides* | | |
	Queens (N = 13)	Workers (N = 92)	ANOVA (F)	Queens (N = 35)	Workers (N = 216)	ANOVA (F)
HW	2.04 ± 0.03	2.01 ± 0.03	7.45***	1.67 ± 0.06	1.66 ± 0.07	0.05
IDm	0.72 ± 0.02	0.72 ± 0.02	0.30	1.09 ± 0.04	1.09 ± 0.06	0.001
GW	0.40 ± 0.02	0.40 ± 0.03	0.01	0.71 ± 0.03	0.72 ± 0.04	0.003
MSW	2.09 ± 0.10	2.06 ± 0.11	0.80	0.94 ± 0.04	0.96 ± 0.04	7.93***
AL	1.19 ± 0.03	1.17 ± 0.03	4.69*	2.08 ± 0.09	2.09 ± 0.11	0.33
T_1L	1.36 ± 0.05	1.31 ± 0.09	2.50	1.47 ± 0.08	1.49 ± 0.08	2.43
T_1BH	0.21 ± 0.03	0.21 ± 0.02	0.01	0.30 ± 0.02	0.31 ± 0.03	4.21*
T_2BW	0.79 ± 0.04	0.77 ± 0.04	1.19	1.32 ± 0.07	1.28 ± 0.07	12.82***
WL	2.38 ± 0.07	2.31 ± 0.09	4.97*	2.07 ± 0.08	2.04 ± 0.08	3.55

| | *Nectarinella championi* | | | *Synoeca surinama* | | |
	Queens (N = 13)	Workers (N = 92)	ANOVA (F)	Queens (N = 26)	Workers (N = 187)	ANOVA (F)
HW	2.13 ± 0.03	2.10 ± 0.027	7.25**	3.88 ± 0.08	3.86 ± 0.10	0.53
IDm	0.92 ± 0.03	0.91 ± 0.022	0.51	1.86 ± 0.05	1.85 ± 0.05	0.94
GW	0.56 ± 0.05	0.57 ± 0.03	0.17	0.99 ± 0.07	0.96 ± 0.07	4.54***
MSW	1.61 ± 0.04	1.58 ± 0.05	1.91	6.03 ± 0.14	5.92 ± 0.43	1.56
AL	2.33 ± 0.11	2.29 ± 0.071	2.04	2.74 ± 0.07	2.72 ± 0.09	2.08
T_1L	1.37 ± 0.11	1.26 ± 0.07	12.02***	3.58 ± 0.14	3.56 ± 0.12	1.06
T_1BH	0.24 ± 0.02	0.25 ± 0.028	1.35	1.18 ± 0.05	1.18 ± 0.06	0.36
T_2BW	1.33 ± 0.06	1.23 ± 0.151	4.40*	1.77 ± 0.07	1.75 ± 0.07	1.75
WL	2.29 ± 0.05	2.31 ± 0.07	1.60	6.68 ± 0.12	6.64 ± 0.18	1.00

***$p < 0.001$; **$p < 0.02$; *$p < 0.05$.

TABLE 5
Means and Observed Values of ANOVA Test, for Nine Characters Used for Discriminating Castes of
Charterginus fulvus, Chartergus metanotalis, **and** *Epipona tatua*

| | *Charterginus fulvus* | | | *Chartergus metanotalis* | | | *Epipona tatua* | | |
	Queens (N = 6)	Workers (N = 22)	ANOVA (F)	Queens (N = 9)	Workers (N = 45)	ANOVA (F)	Queens (N = 46)	Workers (N = 54)	ANOVA (F)
HW	4.49 ± 0.04	4.43 ± 0.05	7.82**	5.64 ± 0.07	5.65 ± 0.07	0.30	3.79 ± 0.06	3.69 ± 0.07	60.3***
IDm	1.60 ± 0.06	1.56 ± 0.04	2.99	2.34 ± 0.05	2.28 ± 0.05	20.75***	1.73 ± 0.04	1.68 ± 0.05	35.2***
GW	0.43 ± 0.02	0.40 ± 0.03	4.53**	0.72 ± 0.13	0.74 ± 0.05	9.87***	0.94 ± 0.05	0.88 ± 0.06	28.7***
MSW	3.38 ± 0.06	3.28 ± 0.07	8.39**	4.40 ± 0.11	4.31 ± 0.08	42.8***	2.68 ± 0.08	2.55 ± 0.08	80.7***
AL	5.75 ± 0.16	5.66 ± 0.16	1.70	7.40 ± 0.20	7.05 ± 0.18	11.27***	7.43 ± 0.19	7.03 ± 0.25	79.1***
T_1L	4.35 ± 0.16	4.09 ± 0.13	17.17***	5.12 ± 0.15	5.01 ± 0.23	1.67	3.25 ± 0.16	3.05 ± 0.17	33.1***
T_1BH	0.63 ± 0.03	0.61 ± 0.03	1.50	0.62 ± 0.05	0.61 ± 0.04	0.50	0.64 ± 0.03	0.61 ± 0.03	27.4***
T_2BW	3.63 ± 0.05	3.50 ± 0.12	7.60**	5.85 ± 0.10	5.83 ± 0.11	37.47***	1.33 ± 0.04	1.27 ± 0.06	33.1***
WL	5.24 ± 0.10	5.14 ± 0.11	4.30*	9.40 ± 0.16	9.00 ± 0.30	0.30	4.42 ± 0.09	4.24 ± 0.13	62.9***

***$p < 0.001$; **$p < 0.02$; *$p < 0.05$.

TABLE 6
Means and Observed Values of ANOVA Test, for Nine Characters Used for Discriminating Castes of *Polybia liliacea*, *Polybia rejecta*, and *Polybia spinifex*

	Polybia liliacea			*Polybia rejecta*			*Polybia spinifex*		
	Queens (N = 84)	Workers (N = 66)	ANOVA (F)	Queens (N = 21)	Workers (N = 79)	ANOVA (F)	Queens (N = 11)	Workers (N = 100)	ANOVA (F)
HW	3.68 ± 0.06	3.81 ± 0.03	200.6***	2.99 ± 0.03	2.95 ± 0.05	21.87***	5.66 ± 0.04	5.44 ± 0.13	32.8***
IDm	1.67 ± 0.05	1.62 ± 0.05	45.7***	1.24 ± 0.03	1.16 ± 0.03	89.9***	2.79 ± 0.07	2.65 ± 0.09	23.11***
GW	0.70 ± 0.05	0.62 ± 0.03	167.9***	0.50 ± 0.04	0.48 ± 0.04	5.14*	1.01 ± 0.04	1.01 ± 0.10	0.01
MSW	2.84 ± 0.08	2.61 ± 0.05	418.5***	2.27 ± 0.05	2.14 ± 0.07	63.4***	3.78 ± 0.04	3.43 ± 0.14	75.95***
AL	6.10 ± 0.14	5.87 ± 0.12	112.8***	4.70 ± 0.08	4.38 ± 0.11	147.01***	8.31 ± 0.10	7.70 ± 0.32	40.22***
T_1L	3.16 ± 0.36	2.91 ± 0.10	29.7***	2.61 ± 0.09	2.42 ± 0.10	65.4***	5.42 ± 0.15	4.99 ± 0.24	33.91***
T_1BH	0.69 ± 0.04	0.60 ± 0.04	208.7***	0.45 ± 0.03	0.41 ± 0.02	25.01***	0.86 ± 0.04	0.79 ± 0.06	15.79***
T_2BW	2.36 ± 0.11	2.07 ± 0.06	380.3***	1.37 ± 0.07	1.23 ± 0.08	58.49***	2.34 ± 0.07	2.02 ± 0.13	66.74***
WL	5.13 ± 0.08	5.07 ± 0.10	14.8***	3.88 ± 0.08	3.73 ± 0.10	44.33***	9.40 ± 0.16	9.00 ± 0.30	18.75***

***$p < 0.001$; **$p < 0.02$; *$p < 0.05$.

to the model that predicts the caste of the individual wasps. Significance values of the loadings of each morphometric variable indicate whether that variable contributes meaningfully to the prediction of caste. Analysis showed that, in the above species, Wilks' lambda values were always high, ranging from 0.7 to 1.0 (table 8). Considering that lambda is defined as 1.0 *minus* the squared canonical correlation, the highest value is 1.0, indicating complete absence of association. These data indicate that morphological castes are practically absent in these species, based on these measures. Specifically, even if queens may differ from workers on average, the ability to identify an individual as a queen or worker based on morphometric values is very poor. None of the queens were correctly classified by discriminant scores in *An. pallens* or *Cl. sulcata*, and relatively few in *L. dorsata*, *M. aztecoides*, *N. championi*, and *S. surinama* (see table 10). Only in *As. ujhelyii* are castes better discriminated.

In a second group (fig. 3)—*Charterginus fulvus*, *Chartergus metanotalis*, *Epipona tatua*, *Polybia rejecta*, and *P. spinifex*—queens were larger than workers. Mean differences using ANOVA (tables 5, 6) were found in five of nine characters in *Cn. fulvus* and *Cg. metanotalis*. In *E. tatua*, *Po. rejecta*, and *Po. spinifex* all body measurements were different.

Multivariate analysis showed that the mea-

surements had a low power of discrimination in *Cn. fulvus*, *Cg. metanotalis*, and *E. tatua* (tables 8, 9), and that discrimination between castes can only occur based on a combination of measurements. In *Polybia rejecta* and *Po. spinifex*, differences were much more pronounced and all measurements were stronger discriminators. Wilks' lambda ranged from 0.1 to 0.3 (table 9), and castes were more clearly discriminated than in the previous group (table 10). ANCOVA showed significant differences in growth rates of body parts in at least one character in all species of this group (table 7).

In a third class, *Polybia liliacea* castes were as clearly distinct as in the second group, but head width was smaller in queens than in workers (table 6). ANOVA showed that all measurements were different between queens and workers.

DISCUSSION

A distinct physiological separation of females into those that are reproductive and those that are nonreproductive is possible based on ovarian condition and insemination in some of the species reported here. While complete absence of ovarian development in workers (i.e., the absence of both types B and C) was not found in the species studied here, such a syndrome has been reported in *Apoica flavissima*, *Agelaia vicina* (Sakagami et al., 1996), *Ag. pallipes*, and *Ag. multipicta* (Noll
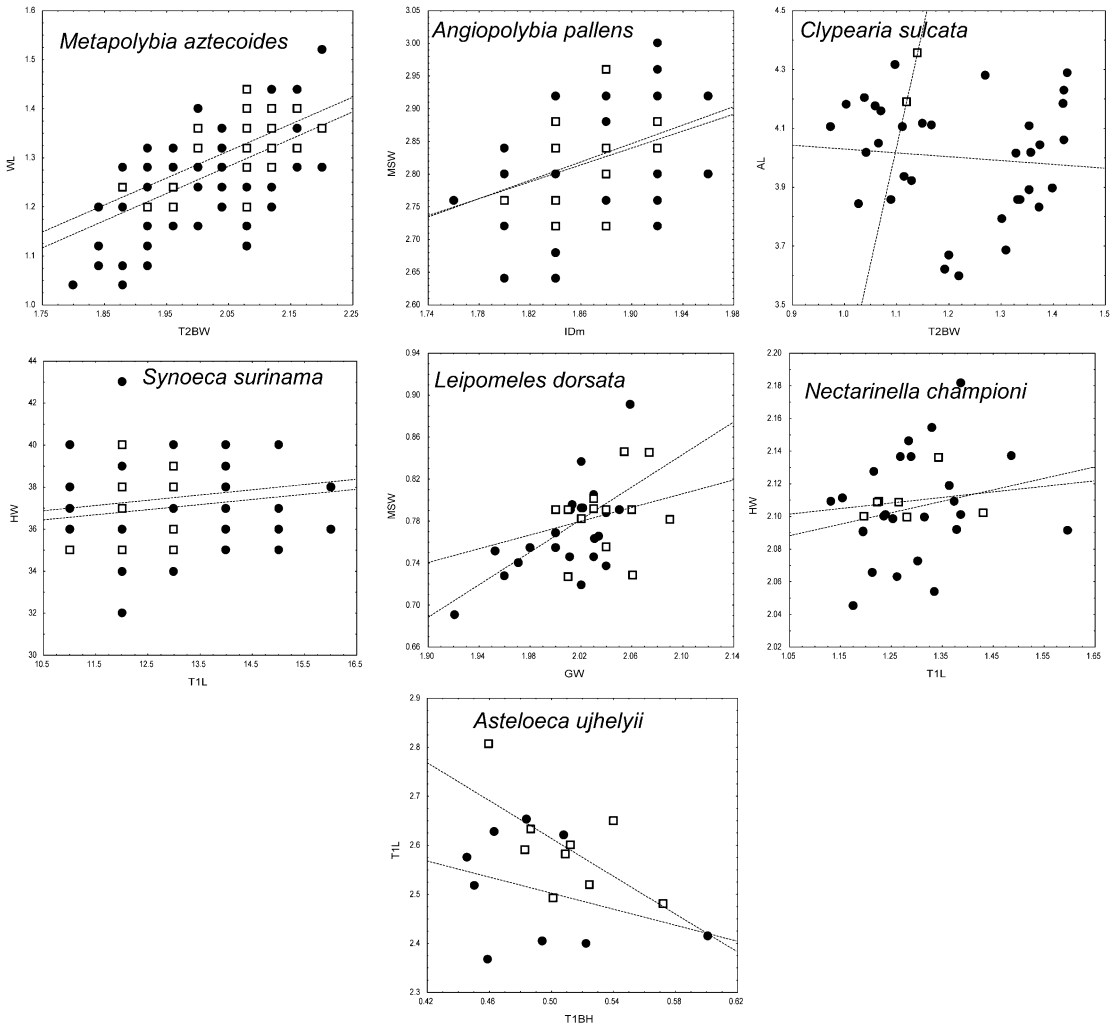
Fig. 2. Slight caste discrimination found in some epiponines based mostly on shape (when applicable). Individuals identified by dissection to be "queens" are represented as squares, while those identified as "workers" are solid dots. Separate regression lines are drawn for illustration only; see text for discussion.

et al., 1997). In our present study, queens' ovaries (type D) were much longer than workers' ovaries in *Chartergus metanotalis*, *Epipona tatua*, *Polybia liliacea*, *Po. rejecta*, and *Po. spinifex*. This situation is also known in *Apoica flavissima* (Shima et al., 1994), *Protonectarina sylveirae* (Shima et al., 1996a), *Polybia dimidiata* (Shima et al., 1996b), *Po. scutellaris*, *Po. paulista* and *Po. occidentalis* (Noll and Zucchi, 2000), *Agelaia vicina* (Sakagami et al., 1996), and *Ag. pallipes* and *Ag. multipicta* (Noll et al., 1997). Similarly, though less discrete, intermediate type C was not found in *Asteloeca ujhelyii*, *Chartergus metanotalis*, *Clypearia sulcata*, *Epipona tatua*, *Metapolybia aztecoides*, *Polybia liliacea*, *Po. rejecta*, *Po. spinifex*, and *Synoeca surinama* (table 2). Other species previously reported to have similar distinction are *Protonectarina sylveirae* (Shima et al., 1996a), *Polybia dimidiata* (Shima et al., 1996b), *Po. scutellaris* and *Po. paulis-*

TABLE 7

Covariance Analyses Using Alitrunk Length as Covariate for the Analyzed Species

ANCOVA F

	Angiopolybia pallens	Asteloeca ujhelyii	Charterginus fulvus	Chartergus metanotalis	Clypearia sulcata	Epipona tatua	Leipomeles dorsata	Metapolybia aztecoides	Nectarinella championi	Polybia liliacea	Polybia rejecta	Polybia spinifex	Synoeca surinama
HW	NS	NS	6.00*	NS	NS	9.89***	7.30**	NS	4.78*	187.43***	0.47	1.50	NS
IDm	NS	NS	NS	2.18	NS	5.75*	NS	NS	NS	3.23	16.55***	0.61	NS
GW	NS	NS	4.70*	NS	NS	9.60*	NS	NS	NS	50.12***	2.96	5.92**	4.50*
MSW	NS	NS	NS	2.17	NS	10.49*	NS	10.49***	NS	201.18***	1.50	26.11***	NS
T_1L	NS	NS	14.35***	NS	NS	7.67**	NS	NS	10.58***	6.17**	1.23	7.79**	NS
T_1BH	NS	NS	NS	NS	NS	0.37	NS	0.37	NS	72.58***	0.12	6.36**	NS
T_2BW	NS	NS	6.54*	9.60***	NS	4.74*	NS	4.74*	2.81	186.02***	9.38***	30.28***	NS
WL	NS	NS	2.56	NS	NS	10.55***	4.34**	10.55***	NS	32.80***	0.02	0.18	NS

Values that were not significant in the ANOVA of table 5 are listed as "NS" and were not tested for significance under the ANCOVA.
***$p < 0.001$; **$p < 0.02$; *$p < 0.05$.

TABLE 8

Wilks' Lambda and F-Statistics

Lambda values estimate the degree of contribution for each separate measure to the final discriminant function model. In these cases values were between 1.0 and about 0.5, indicating low discrimination of castes. F-statistics for ANOVA using the same variables are shown, with appropriate significance values.

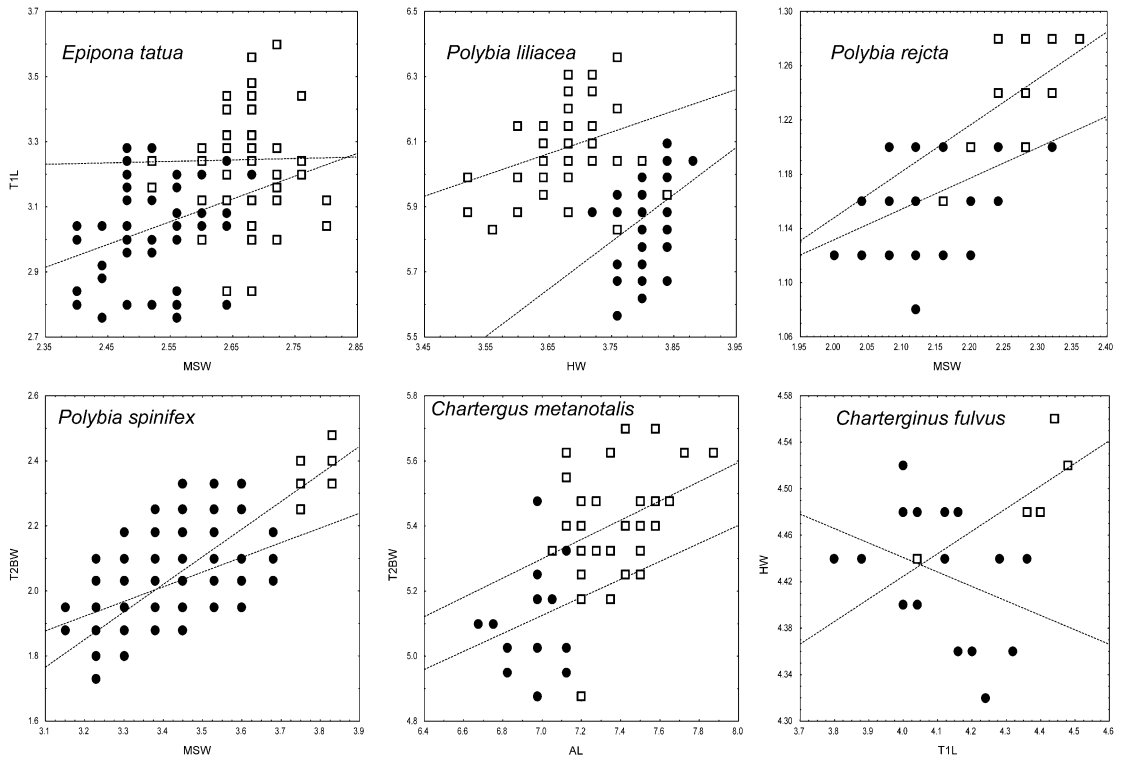|	Angiopolybia pallens		Asteloeca ujhelyii		Clypearia sulcata		Leipomeles dorsata		Metapolybia aztecoides		Nectarinella championi		Synoeca surinama		Charterginus fulvus	
	Wilks' λ	F	Wilks' λ	F	Wilks' λ	F	Wilks' λ	F	Wilks' λ	F	Wilks' λ	F	Wilks' λ	F	Wilks' λ	F
HW			0.89	0.19			0.81	5.17*			0.70	6.41**			0.56	5.03*
GW									0.79	1.66						
IDm	0.99	1.39	0.60	3.47									0.99	3.92*		
MSW	0.99	1.21			1.0	3.79							0.98	1.48		
AL			0.74	7.34**			0.72	1.33	0.82	12.23***	0.72	7.5**				
T_1L			0.78	8.54**			0.75	2.73	0.79	3.67						
T_1BH									0.79	2.80	0.60	1.74				
T_2BW							0.73	1.88	0.84	18.65***					0.72	13.32***
WL									0.84	18.77***					0.49	1.05

***$p < 0.001$; **$p < 0.02$; *$p < 0.05$.

Fig. 3. Caste discrimination found in some epiponines based on size and shape. Individuals identified by dissection to be "queens" are represented as squares, while those identified as "workers" are solid dots. Separate regression lines are drawn for illustration only; see text for discussion.

TABLE 9
Wilks' Lambda and *F*-Statistics
Lambda values estimate the degree of contribution for each separate measure to the final discriminant function model. In these cases values were about 0.5 and lower, indicating better discrimination if compared to those found in table 8. *F*-statistics for ANOVA using the same variables are shown, with appropriate significance values.

	Chartergus metanotalis		Epipona tatua		Polybia liliacea		Polybia rejecta		Polybia spinifex	
	Wilks' λ	F	Wilks' λ	F	Wilks' λ	F	Wilks' λ	F	Wilks' λ	F
HW	0.44	5.54*			0.21	34.78***	0.29	2.64	0.483	1.37
GW							0.35	22.14***	0.492	3.34
IDm	0.41	1.81	0.457	4.15*	0.17	1.53	0.30	4.76*	0.495	3.17
MSW	0.44	5.12*	0.463	5.46**			0.39	37.27***	0.537	13.15***
AL	0.48	10.78**	0.446	1.72	0.19	10.88***				
T_1L	0.42	2.56	0.461	4.98*						
T_1BH					0.18	8.82***				
T_2BW	0.46	8.16**			0.18	5.47**	0.32	11.43***	0.539	13.64***
WL	0.41	2.27	0.447	1.96					0.492	3.53

***$p < 0.001$; **$p < 0.02$; *$p < 0.05$.

TABLE 10
Classification Scores for Group Comparisons Using Discriminant Analysis

Species	Observed classification	Predicted classification		% Correct
		Worker	Queen	
Angiopolybia pallens	Worker	82	0	100.0
	Queen	18	0	0
Asteloeca ujhelyii	Worker	7	2	77.8
	Queen	1	8	88.9
Charterginus fulvus	Worker	22	1	95.7
	Queen	1	5	83.3
Clypearia sulcata	Worker	0	34	100
	Queen	0	2	0
Epipona tatua	Worker	45	9	83.3
	Queen	5	41	89.1
Leipomeles dorsata	Worker	4	19	82.6
	Queen	4	9	69.2
Metapolybia aztecoides	Worker	208	8	96.3
	Queen	23	12	34.3
Nectarinella championi	Worker	3	19	86.4
	Queen	5	5	50
Polybia liliacea	Worker	66	0	100
	Queen	2	42	95.5
Polybia rejecta	Worker	77	2	97.5
	Queen	1	20	95.2
Polybia spinifex	Worker	98	2	98
	Queen	0	11	100
Synoeca surinama	Worker	186	1	99.5
	Queen	4	9	69.2
Chartergus metanotalis	Worker	6	40	87
	Queen	6	62	91.2

ta (Noll and Zucchi, 2000), and *Chartergus globiventris* (Noll and Zucchi, 2002). Some species are found to have individuals representing all four stages, implying a near continuum (but that insemination is always associated with type D ovaries). These species include *Angiopolybia pallens*, *Charterginus fulvus*, *Leipomeles dorsata*, and *Nectarinella championi* (table 2). The same pattern, implying a lack of physiological caste in any meaningful way, was previously found in other species using the same procedure, such as *Chartergellus communis* (Mateus et al., 1999), *Pseudopolybia vespiceps* (Shima et al., 1998), *Parachartergus smithii* (Mateus et al., 1997), and *Brachygastra lecheguana* (Shima et al., 2000).

Ovarian development presents a confusing array of conditions, yet previous researchers have tried to find ways to capture the totality of this variation with some kind of overarching hypothesis of caste that would be applied to all species of Epiponini equally. For example, the concept of cyclical oligogyny invokes demography to provide a process by which individuals may become queens at swarm initiation of colonies, but not later in the colony cycle (West Eberhard, 1978). Colony cycle is known to relate to the degree of morphological differentiation in species that do have marked differences, with differences growing as colonies age (e.g., Noll and Zucchi, 2000, 2002), and comparing mature colonies is now required if one is to argue that

the animals that are sampled actually represent the species' breadth of morphological diversity. Nonetheless, the search for a single explanation of caste (its presence or its ambiguity) in Epiponini is still lacking. We offer here a novel view that relies on returning to the fundamental question of whether caste exists at all. We then integrate the answers to those questions to provide the most coherent view of caste to date, one that does not seek to explain all Epiponini through a single fundamental process.

MORPHOMETRIC DIFFERENCES BETWEEN CASTES

Size divergence is usually regarded as an initial step for the origin of morphological castes in the three main groups of social Hymenoptera (ants, bees, and wasps; Wheeler, 1991). In wasps, caste-related size differences are conspicuous in the Vespinae, but complex in the Polistinae (fig. 4). However, the practice of comparing ratios of linear body measures (fig. 4) may be overly simple to capture the actual patterns of caste determination. For this reason, we used not only linear measures themselves, but also analysis of their covariance to look for shape differences associated with reproductive status as well as size differences.

In general, morphometric differences associated with ovarian status were either slight or absent in *Angiopolybia pallens*, *Asteloeca ujhelyii*, *Clypearia sulcata* (table 3), *Leipomeles dorsata*, *Metapolybia aztecoides*, *Nectarinella championi*, and *Synoeca surinama* (table 4). Other studies found the same for *Parachartergus smithii* (Mateus et al., 1997), *Pa. colobopterus* (Strassmann et al., 1991), *Pseudopolybia vespiceps* (Shima et al., 1998), *Chartergellus communis* (Mateus et al., 1999), *Brachygastra lecheguana* (Shima et al., 2000), *Synoeca cyanea* (Noda et al., 2003), and *Metapolybia docilis* (Baio et al., 2003a). In this group, we might say that while some individuals are reproductive and some are not, there is no meaningful morphological caste. In some cases, caste appears to be what Kukuk (1994) called behaviorally eusocially determined in the adult stage. In *Metapolybia* and *Synoeca* (West-Eberhard, 1978, 1981), caste is apparently determined by disputes

among adults rather than by larval manipulation. Young females have their ovaries suppressed in queen-right colonies, so that only through orphanage do young females develop their ovaries and become queens (West-Eberhard, 1978). In such species, caste as a physiological state may be distinct even if it is impossible to recognize morphologically. Of particular interest may be *Asteloeca ujhelyii*. In table 10 there is fairly good discrimination of reproductive "queens" and nonreproductive "workers", with from 10 or 20% error. Table 8 shows that two values contribute significantly to the discriminant function model, meaning that the computer can find a way to separate reproductives and nonreproductives if they are labeled prior to analysis. However, table 3 shows that none of the linear metrics are significantly different between castes (see also fig. 2 for graphic representation of overlap). Thus, this species presents a kind of intermediate state in which reproductive status can be explained by shape differences after the fact, but not predicted based on the nine morphometric variables independently, including variables that are adequate to capture caste in other species (see below). *Asteloeca ujhelyii* occupies a region of parameter space that represents a shift between species with distinct reproductive castes and those that are casteless morphologically.

Species of Epiponini appear to represent a continuum from those without morphological castes (above) to those with discrete castes (below). There are now enough data to demonstrate this by presenting measures from species analyzed by the same protocols, whether in the present study or in the literature. Plotting the percentage of queens correctly classified by discriminant function analysis (table 10, and literature) versus Wilks' lambda values (table 8 and 9, and literature), we see that in many species queens are classified correctly from 80 to 100% of the time, while in other species classification is less effective (fig. 5). Breaking the continuum of figure 5 into logical parts, we find that species with low Wilks' lambda for morphometric variables (i.e., they show strong covariance between morphometric measures and ovarian status) can be classified correctly most of the time (fig. 5, region A). Distinctions between reproductive and nonreproduc-
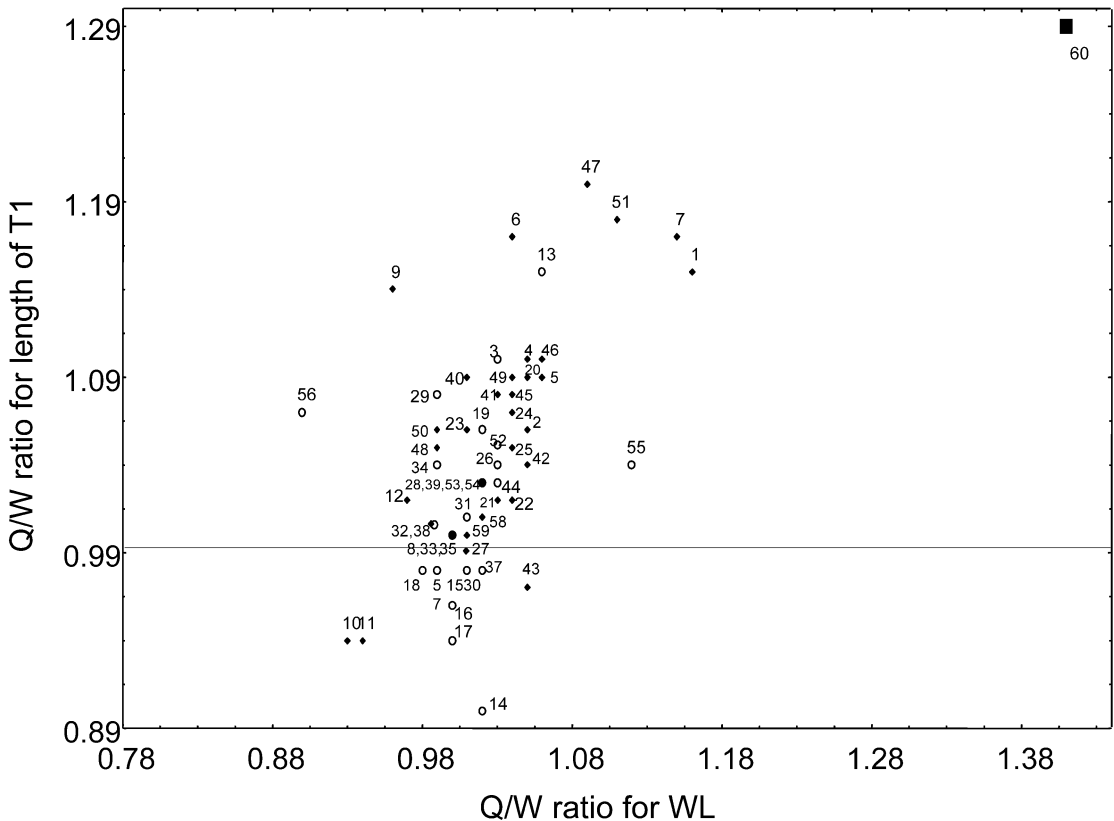
Fig. 4.   Comparison of the level of caste distinction between epiponines (1–59, white circles indicate workers with ovarian development, black diamonds indicate workers without ovarian development) and a Vespinae (60, black square) based on wing length queen–worker ratio versus length of tergite I (except 14, 16, 17, 33–35, 37: hamuli number and 56: width of tergite I). 1. *Agelaia areata*, 2. *A. fulvofasciata*, 3. *A. lobipleura*, 4. *A. multipicta*, 5. *A. pallipes*, 6. *A. vicina*, 7. *A. yepocapa*, 8. *Angiopolybia pallens*, 9. *Apoica flavissima*, 10. *A. gelida*, 11. *A. pallens*, 12. *Asteloeca ujhelyii*, 13. *Brachygastra augusti*, 14. *B. bilineolata*, 15. *B. lecheguana*, 16. *B. moebiana*, 17. *B. scutellaris*, 18. *Chartergellus communis*, 19. *Charterginus fulvus*, 20. *Chartergus chartarius*, 21. *C. globiventris*, 22. *C. metanotalis*, 23. *Clypearia sulcata*, 24. *Epipona tatua*, 25. *E. guerini*, 26. *Leipomeles dorsata*, 27. *Metapolybia aztecoides*, 28. *M. docilis*, 29. *Nectarinella championi*, 30. *Parachartergus colobopterus*, 31. *Pa. fraternus*, 32. *P. smithii*, 33. *Polybia bicytarella*, 34. *Po. bistriata*, 35. *Po. catillifex*, 36. *Po. dimidiata*, 37. *Po. emaciata*, 38. *Po. erythrothorax*, 39. *Po. jurinei*, 40. *P. liliacea*, 41. *P. occidentalis*, 42. *P. parvulina*, 43. *P. platycepha sylvestris*, 44. *P. quadricincta*, 45. *Po. rejecta*, 46. *Po. ruficeps*, 47. *Po. scutellaris*, 48. *Po. singularis*, 49. *Po. spinifex*, 50. *Po. striata*, 51. *Protonectarina sylveirae*, 52. *Protopolybia exigua*, 53. *Pr. minutissima*, 54. *Pr. pumilla*, 55. *Pr. sedula*, 56. *Pseudopolybia difficilis*, 57. *Ps. vespiceps*, 58. *Synoeca cyanea*, 59. *S. surinama*, 60. *Vespula squamosa*. For references for the species, see table 1.

tive females may represent a general increase in all measures (e.g., *Polybia rejecta* or *Po. spinifex*, fig. 3, table 5) or in some measures more than others such that there is a conspicuous shape difference as well (dramatically in *Polybia liliacea*, where queens are larger in all ways, except with smaller heads in absolute terms, fig. 3, table 6). In the mid-

dle of the continuum (fig. 5, region B) are species such as *Asteloeca ujhelyii* with high Wilks' lambdas (weak covariance between measures and ovarian status). These may be without conspicuous size differences (fig. 2, table 3; fig. 5, region B; *Asteloeca ujhelyii*), but shape differences are enough to permit effective classification of reproductives
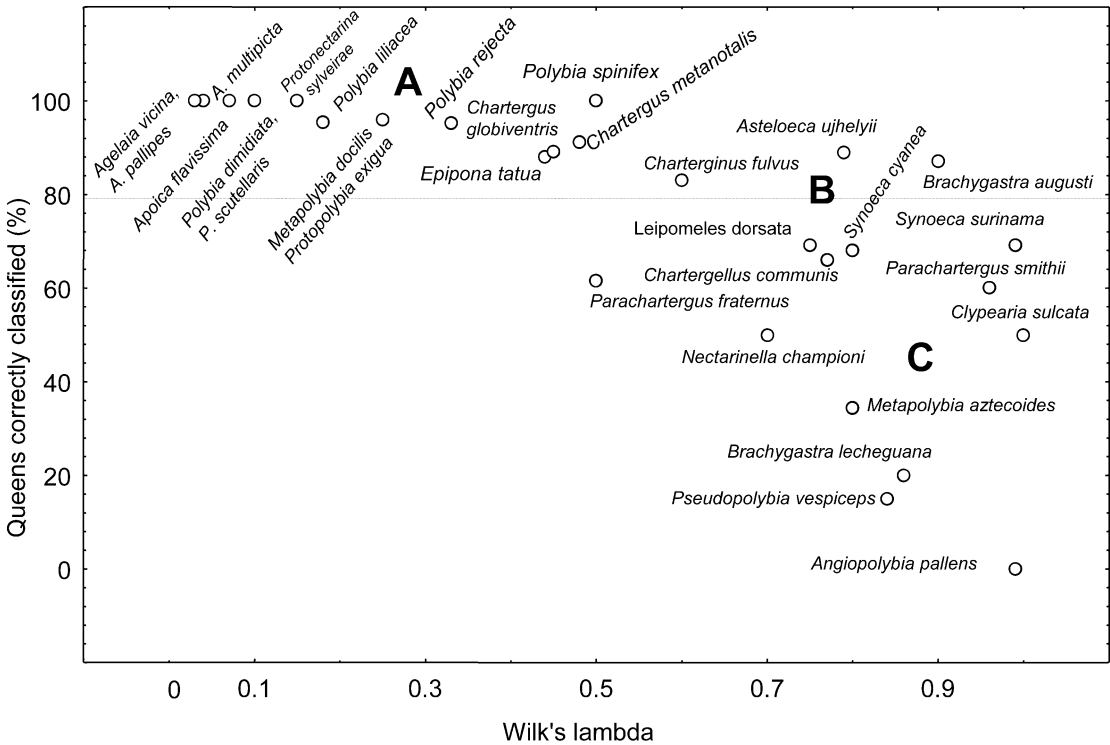
Fig. 5.   Plots of Wilks' lambda values versus queens correctly classified using discriminant function analysis for some epiponines. See text for discussion.

nonetheless. These species that can be correctly classified as queens or workers (fig. 5, regions A and B) show that there is no general rule for identifying reproductives, because the way queens differ in shape from workers varies between species (tables 8, 9). Finally, in some species reproductives do not differ substantially in size or shape (e.g., *Angiopolybia pallens*, table 3, *Nectarinella championi*, table 4; fig. 2 and table 8; fig. 5, region C).

SHAPE: It has long been known that reproductive status in Epiponini is not strongly associated with body size for many species. Indeed, the claim that morphological castes had arisen without a primordial size component was first made for social wasps (Jeanne et al., 1995). Castes in *Apoica pallens* differed significantly in body proportions but not in overall size. Such a finding indicates that morphological castes may not have their origins in a single allometric growth function along a body size gradient (Jeanne et al., 1995). It seems that in *Apoica pallens*, as

well as in several other epiponines (see below), the nature of queen–worker differences would be determined during the larval stage such that queen-destined larvae show different growth rates of various compartments compared to worker-destined larvae, generating animals of different shape even though they are about the same size. In several species, not only shape but also size is involved, perhaps as a secondary acquisition (Jeanne, 1996: Hunt et al. 1996).

Hunt et al. (1996) proposed that shape differences in *Epipona guerini* represent diphasic allometry, which necessarily indicates preimaginal caste determination. Such dimorphism is also known in *Agelaia* (*Ag. flavipennis*, Evans and West-Eberhard, 1970; *Ag. areata*, Jeanne and Fagen, 1974; *Ag. pallipes* and *Ag. multipicta*, Noll et al., 1997; *Ag. vicina*, Sakagami et al., 1996; Baio et al., 1998), *Apoica* (*Apoica flavissima*, Shima et al., 1994; Noll and Zucchi, 2002; *Ap. pallens*, Jeanne et al., 1995), *Chartergus globiventris* (Noll and Zucchi, 2002), *Protonec-*

tarina sylveirae (Shima et al., 1996b, 2003), *Protopolybia* (*Protopolybia exigua*, Noll et al., 1996; Noll and Zucchi, 2002; *Pr. acutiscutis*, cited as *Pr. pumila*, Naumann, 1970), *Polybia* (*Polybia occidentalis*, Richards and Richards, 1951; Noll et al., 2000; *Po. bistriata*, Richards and Richards 1951; *Po. emaciata*, Hebling and Letízio, 1973; *Po. dimidiata*, Maule-Rodrigues and Santos, 1974; Shima et al., 1996a; *Po. paulista* and *Po. scutellaris*, Noll and Zucchi, 2000), and *Pseudopolybia difficilis* (Jeanne, 1996). In the present study, different regression lines for queens and workers indicate different developmental paths in certain species, some more strongly than others. There is clear distinction for *Polybia liliacea* and *Epipona tatua*, somewhat less clear for species where queens are mostly larger, such as *Polybia spinifex*, *Po. rejecta*, and *Chartergus metanotalis*, while regressions for *Charterginus fulvus* are based on relatively few data (fig. 3). Note that the plot of *Epipona tatua* closely matches that of *E. guerini* from Hunt et al. (1996), so although the evidence for preimaginal determination in *Epipona* is less distinct than for certain other species (say, *Polybia liliacea*), it is found in different species of the genus and therefore is probably real.

INTERMEDIACY: Even though preimaginal caste determination is well documented in a number of species (above), in others reproductive and nonreproductive females cannot be distinguished by morphology. Ovarian status itself may also be continuous such that there is no discrete separation of females. Richards and Richards (1951) referred to noninseminated females with developed ovaries as "intermediates". Uninseminated layers can be found in species with some morphological caste differentiation such as *Protopolybia exigua* (fig. 5; Simões, 1977; Noll et al., 1997) so that these females are clearly workers (fig. 5). West-Eberhard (1978) suggested that females of worker status would benefit by keeping their ovaries active, even if all their eggs were eaten, because laying workers could attempt to be new queens in the next colony founded by absconding or normal swarms. However, in species where castes are indistinct to begin with (e.g., *Brachygastra lecheguana*, fig. 5, Shima et al., 2000), intermediates present a challenge

to the concept of caste itself because they further obscure the difference between reproductives and nonreproductives. After all, there can be no meaningful "caste" if there is no meaningful difference between females. As mentioned above, terms such as "laying worker" or "replacement queen" do not serve to clarify the situation if worker and queen castes are not already distinct. Strassmann et al. (2002) named the situation in which any female may possibly become an egglayer in the event of loss of some queens as "caste totipotency". The term is somewhat of an oxymoron if "caste" itself means anything. The problem is that the concept of caste is being stretched to mean different things in different situations.

SYNTHESIS: Reproductive castes are not the same from species to species in Epiponini. Some interpretable patterns form when we capture the diversity in terms of simple morphometrics (fig. 5), but there is little explanatory power in a plot of canonical covariance and reproductive status. This is partly because the details of evolution are overspecified in the morphometric data. For example, the idea that queens should have proportionally larger abdomens and smaller heads is both classical and logical (Jeanne and Fagen, 1975; Yamane et al., 1983), but it does not specify which dimensions of the head or abdomen should change most noticeably. Similarly, Wheeler's (1991) model stated that isomorphic species would develop size-based differences in developmental patterns, but it does not specify what body dimensions will differ to fulfill diphasic allometry. Wheeler's model would be considered valid if different measures in different species satisfied the prediction, because the model is based on the evolution of a syndrome (i.e., the evolution of a number of different characters that are expected to change in loose synchrony). To interpret the current data, we need to reduce the details of our analysis to compose syndromes so that the broad patterns of evolution are not lost in the metric details. Table 1 represents just an effort at defining syndromes, with categories following Richards' (1978) concepts based on individual measures. However, our treatment of the covariance terms and intermediate females (see the discussion of fig. 5, and above) permits us to
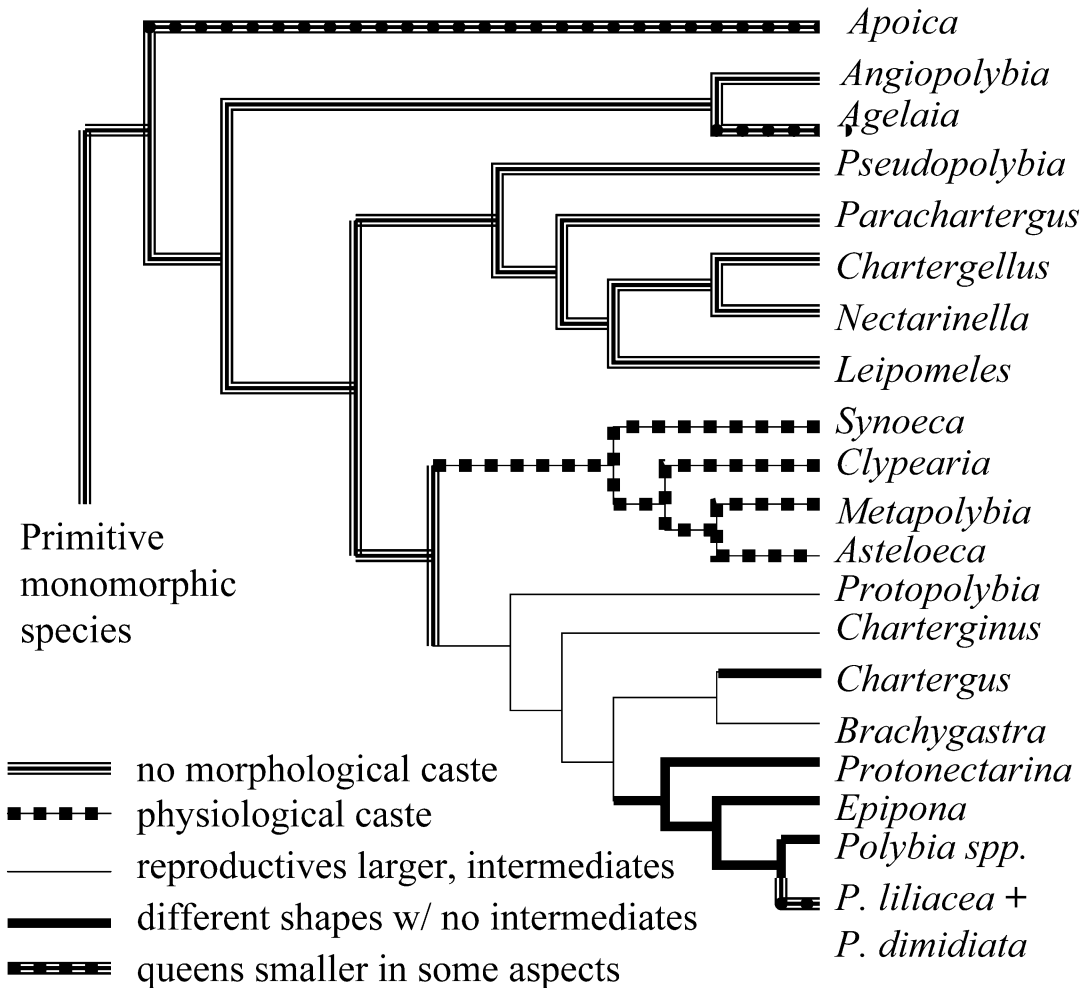
Fig. 6. Caste syndromes defined by data of table 1 and ovarian dissection, optimized on cladogram of Wenzel and Carpenter. Where genera are polymorphic for caste syndrome, terminals are coded according to parsimonious optimization.

reformulate Richards' syndromes and add one more. We propose the following groups: (1) *casteless* (no size or shape difference associated with reproduction, females of all ovarian conditions present); (2) *physiological caste only* (no morphometric differences, but ovarian condition unambiguous by absence of type C females); (3) *queens larger* but mostly the same shape; (4) *queens shaped differently* with some measures smaller than workers. Although further research may find this list (or characterization of given species within the list) to be incomplete, we show

below that a powerful and coherent pattern emerges from this perspective.

Figure 6 represents the working cladogram to date for Epiponini, from the cladogram of Wenzel and Carpenter (1994), rooted to a hypothetical ancestor that is without morphological caste (*Polistes*, *Mischocyttarus*, etc.). Generic synonymies published since 1994 have been incorporated here (*Clypearia* = *Occipitalia*, Carpenter et al., 1996; *Polybia* = *Synoecoides*, Carpenter et al., 2000; *Leipomeles* = *Marimbonda*, Carpenter, in press). The original cladogram was reported

from analysis of Carpenter's (1991) morphological matrix of 31 characters (including a few traditional behavioral characters) and from Wenzel's (1993) matrix of 21 behavioral or nest architectural characters, not overlapping with those of Carpenter. None of the matrix characters included information about caste. The relevant caste syndromes, as defined above, are plotted on the cladogram and optimized parsimoniously to hypothetical ancestors. While figure 5 suggests a spray of points in a continuum, the historical lineages are marked rather neatly in blocks in figure 6. The Epiponini in general is characterized as primitively casteless. Retaining this primitive absence of caste, *Angiopolybia pallens*, *Pseudopolybia vespiceps*, *Parachartergus fraternus*, *P. smithii*, *Leipomeles dorsata*, *Chartergellus communis*, and *Nectarinella championi* all have high Wilks' lambda value and poor queen–worker distinction (fig. 5). Without clear morphological caste, *Synoeca*, *Clypearia*, *Asteloeca*, and *Metapolybia aztecoides* have distinct physiological differences (but notice morphological variation in *M. docilis*, fig. 5). This is the syndrome we have added to Richards' three, and if it were simply synonymized with "no morphological difference" then the absence of caste is even more definitively shown to be the ancestral condition for Epiponini. Some *Polybia* and related genera have queens larger, and a few species of *Polybia* have queens with some dimensions smaller, the final syndrome. This last syndrome is also found in *Apoica* (table 1). *Agelaia vicina*, *Ag. pallipes*, *Ag. multipicta*, and other species in the literature (table 1) also have developed queens of different shape.

The most conspicuous feature of figure 6 is that the interpretation of caste is rather simple. Interestingly, the syndromes as defined by morphological and physiological distinctions map rather neatly to traditional groups as recognized by gross nest architecture. At the foundation are the genera that have covered nests and brood combs supported by pedicels ("calyptodomous, stelocyttarus" Richards, 1978; Wenzel, 1993; *Angiopolybia* to *Nectarinella*). The genera that build with cells directly on the substrate (*Synoeca* to *Asteloeca*, the "astelocyttarus" design of Richards) have physiological caste

only, while the more apical "phragmocyttarus" nest builders have the more sophisticated caste systems. If the syndromes themselves are used as a character of the taxa and combined with the matrices of Carpenter (1991) and Wenzel (1993), then different trees result. Figure 7 shows the principal difference, which is that *Apoica* and *Agelaia* become sisters in a lineage basal to the remainder of Epiponini. This is because the shape difference of queens is enough to unite them, and it constitutes a more parsimonious plot, with only two derivations of queens smaller in some measure than workers, one in the *Apoica-Agelaia* lineage and one in *Polybia liliacea* + *Po. dimidiata*. Future research will test if *Apoica* and *Agelaia* are actually sisters. It seems that different models offered by Wheeler (1991) and Jeanne et al. (1995) are both fulfilled in different parts of the cladogram, and that one syndrome has not been accounted for in previous models. The proposal from Jeanne et al. (1995) is fulfilled in that *Apoica* derived queens of different shape without first developing different size, either alone (fig. 6) or with its sister *Agelaia* (fig. 7), which may have derived size differences independently.

Wheeler's (1991) more extensive model is fairly direct and general. Our explanation is derived simply from hers. Wheeler started with monophasic variation, meaning that the same allometric relationships operate across a continuous spread of sizes (fig. 8A). One can imagine that the first step to distinct castes is that the continuity in size is interrupted, producing individuals that differ in size and perhaps in behavioral role (fig. 8B). Once this distinction becomes regular, then it would be easy to select for developmental switches that create different allometric relationships in the two size classes, meaning that the large and smallbody-size classes differ in fundamental shape, as well as in size, generating discrete and disjunct variation (fig. 8C). As the efficiency of the switch is improved by operating earlier in development, final gross body size may become irrelevant, and castes could be produced such that they differ in morphology but not in size (fig. 8D). Such switches are already known in *Apis*, where the fate of a larva is determined early, and final body size is not causal
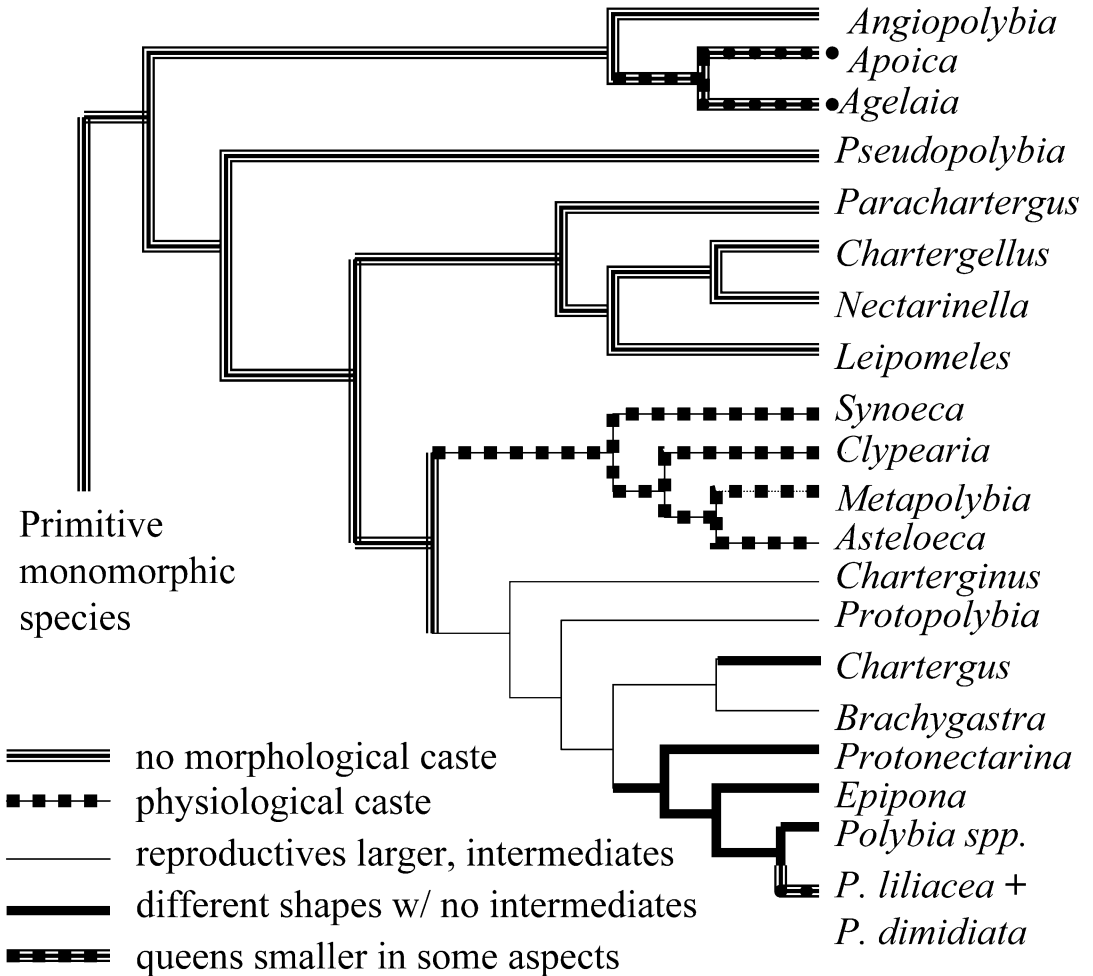
Fig. 7.   Caste syndromes defined as in fig. 6, optimized on cladogram produced by using caste syndrome as a character in combination with the matrix of Wenzel and Carpenter.
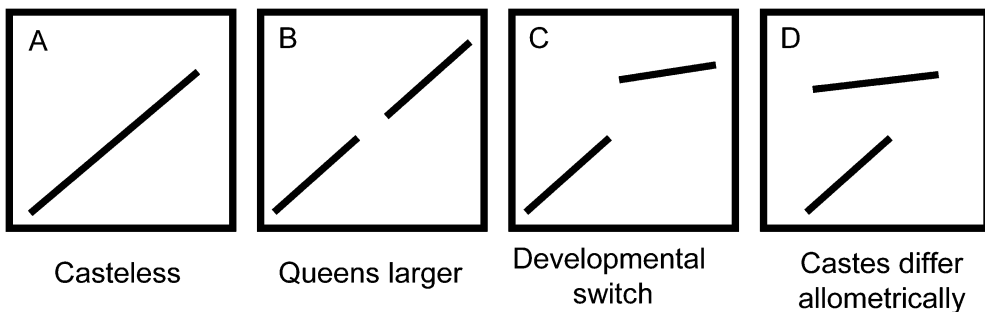

Fig. 8.   Wheeler's (1991) model of the evolution of caste, stepwise in graphical terms, representing morphometric variation measured within a colony. See text for explanation.

to caste determination (Evans and Wheeler, 1999). The presence of the predicted developmental switch in *Apis* is encouraging, but the best corroboration of the model would be to find evidence of the same stepwise procedure as outlined above in a rich dataset. Our cladograms (figs. 6, 7) with caste syndrome optimized on them provide exactly this opportunity. Tracing along the bottommost lineage, which subtends the major path of genus-level diversity, demonstrates that in social wasps there does appear to be stepwise development of the sort necessary to corroborate the model. Casteless societies give rise to those that differ in size, which give rise to those that differ in shape, and some of these include queens that are smaller (hence, a dissociation of size and morphological identity). Thus, the patterns we describe here include the predictions of Wheeler's model, even considering the necessary placement of intermediate states. We think that this is the first empirical validation of Wheeler's model to date.

Neither models by Jeanne et al. (1995) nor Wheeler (1991) anticipated the discovery of "physiological caste only" as reported here, a group where ovary development is clear, with no persistent intermediates. The clade that includes *Synoeca* and *Asteloeca* (fig. 6) has rather distinct reproductives upon dissection, but discrimination is weak based on our measures. These results are difficult to interpret, but the cladistic coherence of the syndrome suggests that it is not an artifact. To propose that this result is somehow erroneous is a great stretch, because that would require that it is only accidental that multivariate statistics find similar patterns among measures from different colonies in different genera in different studies; that it is accidental that only these species were united despite a field of other possibilities; that it is accidental that these species all fall out in a cladistically interpretable pattern; and accidental that this pattern matches that of the traditional "astelocyttarus" nest architecture (see Wenzel [1991, 1993, 1998] for discussion of nest form). The physiological switch that determines reproductivity in this group is not yet understood, but "cyclical oligogyny" was discovered in this group and may provide a key. West Eberhard (1978) reported

that queen number in *Metapolybia* is reduced in part through workers challenging queens, and this may eliminate intermediate females as well if the selection criterion is based on an estimate of fecundity. As such, queen selection by workers would seem to represent an important social behavior that produces selection pressure to have an abrupt switch from nonreproductive to reproductive, and in this clade it is separate from considerations of size or shape, unlike *Polybia* and other derived genera. Organization of labor in *Metapolybia* is also known to differ from that of *Polybia*, being more simple (Karsai and Wenzel, 1998; cf. Jeanne, 1986), and perhaps this "astelocyttarus" clade has been overlooked for important transitional forms in other ways as well.

CONCLUSIONS

This analysis indicates that caste has evolved in different ways in different lineages of Epiponini, starting from casteless societies. Our decision to call the basal condition "casteless" relies on two independent lines of argument. The first argument is that females do not differ meaningfully either in morphology or physiology. The second is that the reproductives do not represent dominant animals, as they do in more primitive societies such as those of *Polistes* and *Mischocyttarus*. As discussed above, workers are known to police the egglayers in *Apoica*, *Synoeca*, and *Metapolybia*, whereas the egglayer herself polices the brood comb in *Polistes*. Thus, the egglayers of the genera represented by the groups of *Angiopolybia* through *Nectarinella*, and *Synoeca* through *Asteloeca* do not represent the same social role as egglayers in *Polistes*; instead, they are simply individuals that lay eggs in a society of females that are not otherwise distinguished. This may not have been recognized before because, despite universal acceptance of Hamiltonian perspectives regarding inclusive fitness, the community of vespid researchers still imagines wasps engaged in a struggle for direct fitness rather than joined in a society of inclusive fitness. It seems likely that different types of socio-regulation exist in epiponines as suggested by Noll and Zucchi (2002). It is possible that some con-

fusion results in the literature from a desire to find a single syndrome to be representative of the entire diversity of swarming wasps, whereas the actual evolution of caste has perhaps been multifaceted.

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