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Caste differences and morphological skew in the swarm-founding wasp *Agelaia timida* Cooper, 2000 (Hymenoptera, Vespidae, Epiponini)

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ABSTRACT

Here, we tested the application of morphological skew in *Agelaia timida* by reporting caste dimorphism and comparing it with other epiponine species. A description of a nest of *A. timida* is also provided. Females were measured to investigate morphological differences between castes and dissected to assess ovarian development. Three types of ovaries were found: filamentous (workers), developed with some mature oocytes (intermediates), and developed and inseminated (queens). Queens are bigger than workers, but discriminant analysis showed castes are not morphologically distinct. Mahalanobis distance showed a statistical separation between inseminated and non-inseminated females, and the only distinct group was workers. The results differ from other species of *Agelaia*, which present clear-cut caste differences. Thus, *A. timida* fits into morphological skew theory since it forms small colonies with low caste differentiation and nonsterility of workers. These features, plus the presence of a true envelope, may be plesiomorphic, as observed in the ground plan of Epiponini.

INTRODUCTION

The origin and the maintenance of a sterile caste has been one of the main problems of the theory of natural selection, dubbed *Darwin's dilemma* by West-Eberhard (1996). Excepting a

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few cases, workers are partly sterile, so they combine typical behaviors of the sterile caste (like food collection, brood care, defense, and nest construction) with some type of reproduction, originating the various patterns found in the Hymenoptera (Bourke, 1988). In fact, as previously predicted by kin selection theory, workers' sterility is conditionally expressed and reveals the variation of genetic interests of the colony (Queller and Strassmann, 1998).

Even though the population size of the mature colonies can be determined at least partially by ecological factors, changes in the number of individuals in a colony can have very important social consequences (Jeanne, 1991; Alexander et al., 1991; Bourke, 1999). The most important of these is the predicted change in the reproductive potential of the workers. As suggested by Bourke (1999), as the colony size increases, workers experience a decrease in their chances of becoming reproductive substitutes, so they increase mutual reproductive inhibition: *worker policing* (Ratnieks, 1988). Once the workers' reproductive potential decreases, the level of reproductive dimorphism between castes increases (Wilson, 1971; Michener, 1974; Oster and Wilson, 1978; Hölldobler and Wilson, 1990; Alexander et al., 1991; Wheeler, 1991). That sort of *morphological skew* (Bourke, 1999) would help explain why societies composed of a few individuals have small differences between castes, and those with many individuals present a more pronounced distinction. For these reasons, small societies would be characterized by a direct conflict between reproduction and caste determination. In contrast, conflicts in larger societies should be predominantly over brood composition, and the members of these societies should be relatively more "resigned" to the manipulation of their castes (Bourke, 1999). In this way, colony size deserves an ampler consideration as a determinant, like kin structure, social complexity, workers' reproductive potential, levels of caste differentiation, and the nature of social conflicts (Bourke, 1999).

The swarm-founding epiponine wasps represent an ideal subject for studying morphological skew because caste differentiation differs from null to complete dimorphism, and worker reproduction is widespread (Noll et al., 2021). In two cases, morphological skew theory applies to these wasps. Some species present small colony size, and slight or indistinct morphological differences and all individuals present consistent ovarian development[4] [*Parachartergus smithii* (Mateus et al., 1997), *Pseudopolybia vespiceps* (Shima et al., 1998), *Chartergellus communis* (Mateus et al., 1999), *Brachygastra augusti* (Baio et al., 2004)]. Other species present larger colonies, castes quite distinct based on allometric differences and worker sterility [*Agelaia. flavipennis* (Evans and West-Eberhard 1970), *A. areata* (Jeanne and Fagen, 1974), *A. vicina* (Sakagami et al., 1996; Baio et al., 1998), *A. pallipes* and *A. multipicta* (Noll et al., 1997a), *Protonectarina sylveirae* (Shima et al., 1996a ; Tanaka et al., 2010), *Polybia scutellaris* (Noll et al., 1997b), *Epipona guerini* (Hunt et al., 1996), *Apoica flavissima* (Shima et al., 1994) and *A. pallens* (Jeanne et al., 1995)]. However, at first glance, two other unusual patterns cannot fit into morphological skew theory. Some species have large colony sizes, allometric caste differences, and the presence of uninseminated egg layers [*Protopolybia exigua* and *P. acutiscutis*, Simões (1977),

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[4] In epiponines, females with ovarian development but non-inseminated were called intermediates by Richards and Richards (1951). For convenience, females will be treated as queens (ovarian development and insemination), workers (ovaries not developed and not inseminated) and intermediates (ovarian development and non-inseminated)

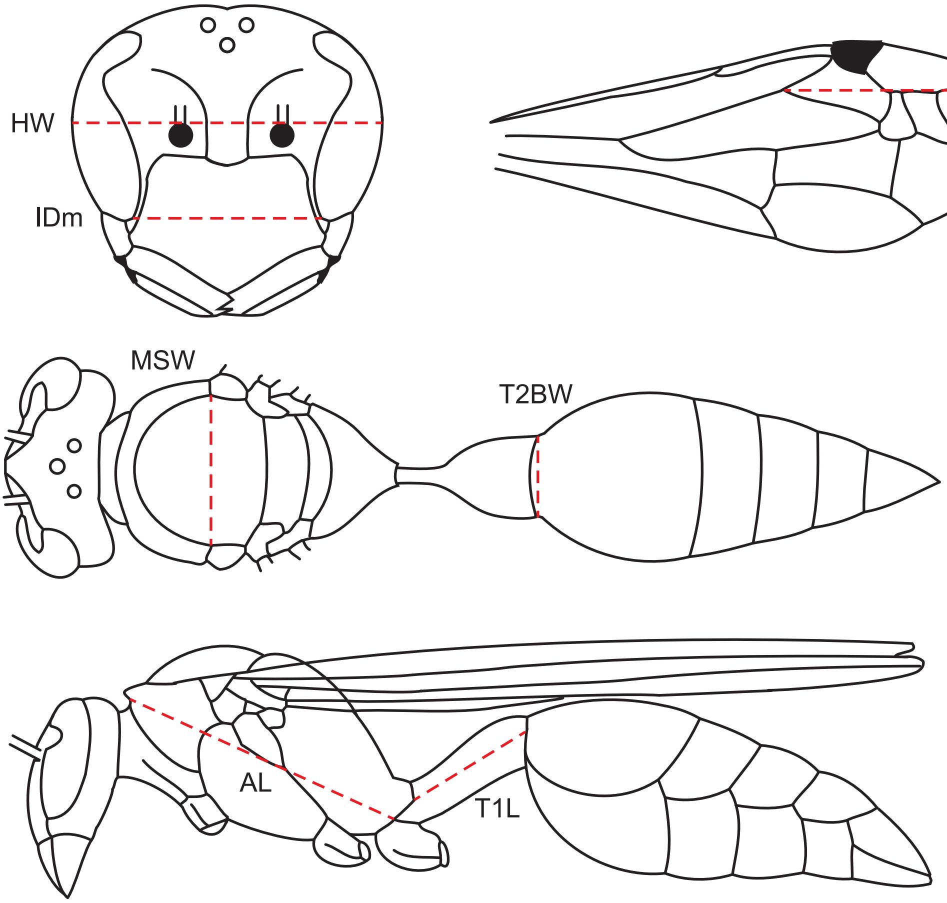

FIGURE 1. Representative scheme of the seven measures for morphometric analyses. Head: **HW,** head width, **IDm,** minimum interorbital distance; Wing: **WL,** partial length of the forewing; Mesosoma: **MSW,** width of mesoscutum, **AL,** alitrunk length; Metasoma: **T1L,** length of gastral tergite I, and **T2BW,** basal widths of tergite II. Modified from Noll and Zucchi, 2004.

Naumann (1970)], while others have small colony sizes, low caste differentiation, and worker sterility [*Metapolybia aztecoides* (West-Eberhard, 1978)].

The genus *Agelaia* Lepeletier, 1836, is a conspicuous part of the social wasp fauna in much of tropical America (Jeanne, 1991), presenting 31 extant species and one fossil species recorded from Dominican amber (Andena et al., 2024; Carpenter and Grimaldi, 1997). Species vary in features such as nest architecture and number of individuals. There are species with small colonies, and species such as *Agelaia vicina*, with colonies harboring hundreds of thousands of individuals (Zucchi et al., 1995). There is a clear dimorphism between queens and workers (Cooper, 2000). In general, compared with workers, queens are larger, the dorsal pronotal carina, when developed, is blunter; the valvula shorter and with a narrower, hyaline border and tergum I wider (Richards, 1978; Noll et al., 1997a; Cooper, 2000). *Agelaia* species typically build their nests in cavities, subterranean or arboreal (Wenzel, 1998). Since the nests are hidden in the majority of species, the presence of an envelope is not the common pattern. *Agelaia areata* and *A. flavipennis* build an exposed nest of a

TABLE 1. Morphometric differences. Means, *t*-test for difference between queens and workers of seven characters used for discriminating the castes of *Agelaia timida*. Head: **HW,** head width, **IDm,** minimum interorbital distance; Wing: **WL,** partial length of the forewing; Mesosoma: **MSW,** width of mesoscutum, **AL,** alitrunk length; Metasoma: **TIL,** length of gastral tergite I, and **T2BW,** basal widths of tergite II. * = All values statistically significant (P <0.01); N.S. = not statistically significant.

	Characters	**Queens (n = 7)**		**Workers (n = 33)**		**Bonferroni *t*- test***	**Wilks' Lambda**	**F**
Head	HW	4.16	0.05	4.00	0.09	4.72	N.S.	
	IDm	1.70	0.05	1.63	0.06	2.91	N.S.	
Mesosoma	MSW	2.71	0.07	2.60	0.10	2.98	N.S.	
	AL	5.96	0.16	5.60	0.21	4.28	N.S.	
Metasoma	T1L	3.35	0.14	3.11	0.17	3.52	N.S.	
	T2BW	1.63	0.05	1.52	0.06	4.51	N.S.	
Wing	WL	6.50	0.11	6.03	0.26	4.57	0.63	10.66*

single spiral comb with the cells on the inside so that the outermost part of the comb functions as an envelope (Jeanne, 1973; Cooper, 2000). A true envelope is found only in *A. timida* and *A. baezae.*

Here, we test the application of morphological skew theory (Bourke, 1999) in epiponines by reporting caste dimorphism in *Agelaia timida* Cooper, 2000, and comparing it with other *Agelaia* and other epiponine species. We also provide a description of a nest of *A. timida*.

MATERIAL AND METHODS

The analyzed colony of *Agelaia timida* were collected in Petit Saut, French Guiana (AMNH_HYM 00000494). The colony was in a mature stage, characterized by the presence of different-aged brood (workers) and at least one adult generation (Noll and Zucchi, 2000, 2002), and all the adult wasps were fixed in alcohol. Forty females, from a total of 53, were randomly selected for measurements and dissections. Seven body parts (fig. 1) were measured under a binocular microscope with an ocular micrometer (smallest unit = 0.0875 mm): head width (HW), minimum interorbital distance (IDm), width of mesoscutum (MSW), alitrunk length (AL), length of gastral tergite I (T1 L), basal width of tergite II (T2BW), and partial length of the forewing (WL). Ovarian condition (number of ovarioles and development of oocytes) and insemination were determined by dissection under a stereomicroscope. The presence of sperm cells was confirmed by microscope.

Before statistical analysis, data were converted by log transformation in order to avoid problems of variance. Two groups, those with ovarian development and insemination (queens) and the remaining females (workers and intermediates), were determined for statistical purposes. Means and standard deviations were calculated from the seven morphological measurements. Bonferroni t-test was used for mean comparisons. The contribution of each variable to caste discrimination was examined using discriminant function analysis with the stepwise method (Rao, 1973).

In order to detect a correlation between caste differences and colony size, Mahalanobis distances (Anderson, 1958) from several epiponines from the literature were used. Mahalanobis

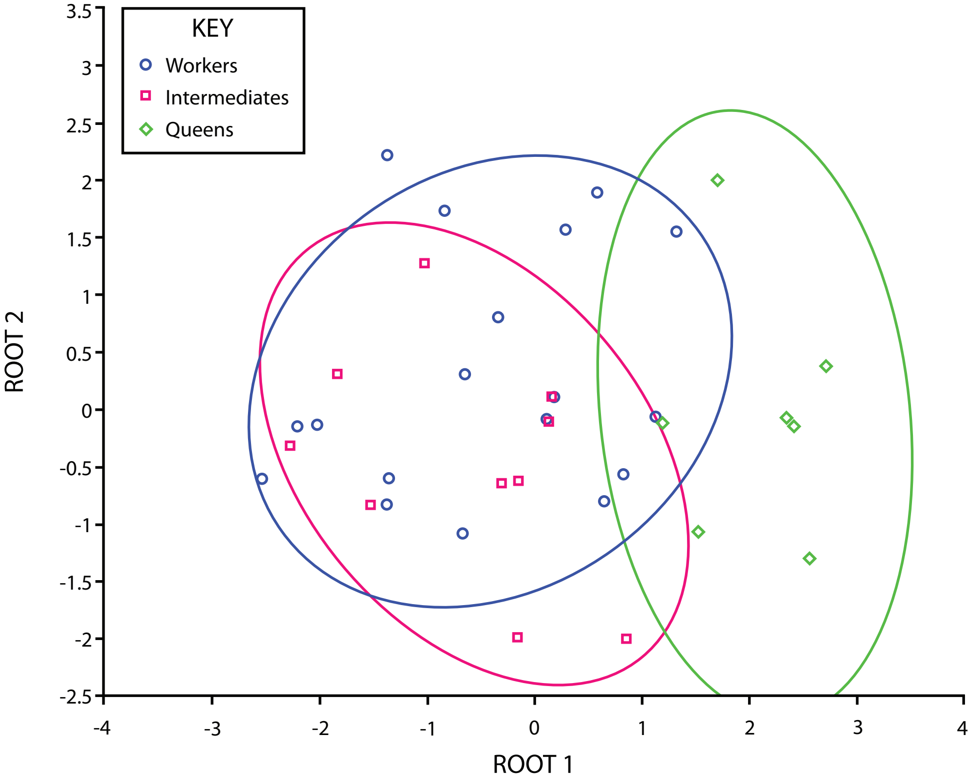

FIGURE 2. Dispersion diagram showing the differentiation among females with the three types of ovarian development recognized (predicted groups according Mahalanobis distance values).

distance between the group centroids is similar to the standard Euclidean distance measure, except that it accounts for the correlations between variables. The larger the differences, the farther are the respective groups apart from each other and the more discriminatory power our current model possesses for discriminating between the respective two groups. Statistical analyzes were performed using Statistica software (v. 12.5). A detailed description of a nest of *Agelaia timida* is also given. The nest is deposited at American Museum of Natural History (Nest 091203-1). It was collected in 2009 in Petit-Saut, French Guiana, by A. Dejean.

RESULTS

Ovary Development and Spermathecal Contents

The adult population comprised 53 females, of which 40 were examined. The ovariole number was always three in each ovary, and three types of ovarian development were documented: type A (n = 20) with filamentous ovarioles, which had no visible oocytes, or with some very small oocytes (workers); type B (n = 13) bearing some young oocytes or with one or more

TABLE 2. Discriminant analysis among castes. Classification results for group comparisons through discriminant analysis in *Agelaia timida* (predicted groups according Mahalanobis distance values).

Observed classifications	**Percent Correct**	**Predicted classifications** **Workers (p = 0.51)**	**Intermediates (p = 0.31)**	**Queens (p = 0.18)**
Workers	85	17	3	0
Intermediates	25	9	3	0
Queens	85,7	1	0	6
Total	66,7	27	6	6

mature oocytes in each ovariole (intermediates); type C (n = 7) with well-developed and very long ovarioles with at least one mature egg, which was contorted inside the metasoma. Insemination was confirmed only in females with type C ovaries, i.e., queens.

Morphometric Queen-Worker Differences

In all measurements, values were statistically different between queens and workers (true workers plus intermediates) (Bonferroni *t*-test, $p < 0.01$; table 1), indicating that queens are larger than workers. However, using multivariate statistics, discriminant function analysis showed only wing length (WL) was included in the model (Wilks' lambda = 0.63; F = 10.66). Also, considering that the highest value is 1.0 (or complete absence of discrimination), these results suggest that castes are not clearly distinct because different measurements are necessary to discriminate castes.

Comparing females with the three types of ovarian development recognized, Mahalanobis distances calculated were 3.47 ($F = 15.8$, $P < 0.001$) between queens and workers, 4.7 ($F = 18.23$, $P < 0.001$) between queens and intermediates, and 0.09 ($F = 0.66$, $P < 0.42$) between workers and intermediates. These values indicate statistical separation between inseminated (queens) and non-inseminated (workers and intermediates) females, showing workers and intermediates were not significantly different. In addition, comparing actual groups with predicted groups through discriminant analysis (table 2, fig. 2), queens are a more distinct group (85.7%) with only one female falling in the predicted worker group. Intermediates cannot be considered as an independent group because only three females (25%) fell in the actual predicted group, and the other females are scattered in the worker predicted group. It also suggests that intermediates are not queens, but a worker phase as suggested by Simões (1977).

Nest Architecture

Agelaia timida is one of the few *Agelaia* species that build a true envelope surrounding their nests (also *A. baezae*), which sets them apart from most species within the genus (Cooper, 2000).

The nest was built on the surface of a tropical plant leaf, and another leaf was used as part of an envelope (fig. 3), which has not been previously reported for the genus (Wenzel, 1998). The vegetable fibers seem to come from the same type of plant, which differs from other *Age-*

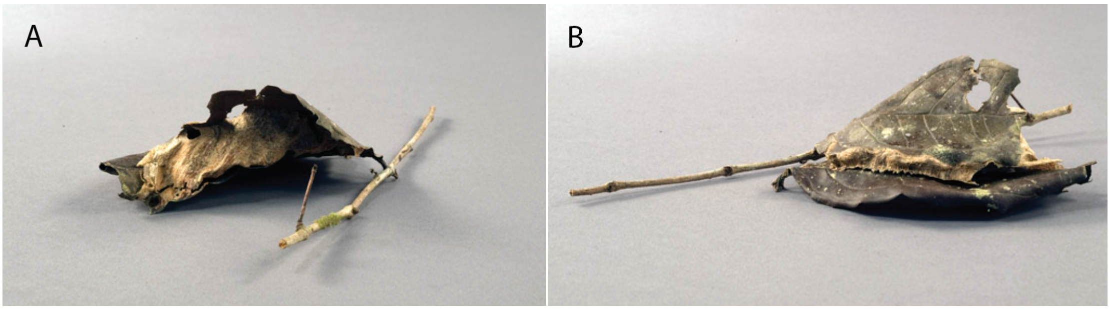

FIGURE 3. Nest of *Agelaia timida* built on the surface of a leaf, and another leaf was used as part of an envelope. **A,** Frontal and **B,** back views (considering the surface where the brood comb is initiated).

laia, which may use several types of plants (Wenzel, 1998). Compared to the envelope of *A. baezae*, the envelope of *A. timida* seems to be more fragile.

Another difference is related to the entrance to the nest. In the nests of *A. baezae*, the entrance is always positioned at the end of the envelope facing downward (toward the ground). In *A. timida*, on the other hand, the entrance is positioned almost in the central area of the envelope. However, three nests of *A. timida* were previously described by Cooper and, in two of them, the entrance was positioned at the distal end (Cooper, 1986, 2000).

It is interesting to note that a nest with similar characteristics was described and illustrated by Wenzel (1998) but attributed to a species of *Marimbonda* (today synonymized with *Leipomeles*).

DISCUSSION

In neotropical swarm-founding wasps, caste differences can be arranged along a spectrum ranging from taxa in which queens and workers are externally similar, lacking morphological differences, to others with fairly distinct caste attributes (Richards, 1978; Jeanne, 1980; da Silva et al., 2021).

According to several authors (reviewed in Noll et al., 2004) caste differentiation in the Epiponini is most developed in *Agelaia*. Most of the species of this genus present the clear-cut case, in which morphological differences between castes are constant, and queens are always distinct from workers throughout the colony cycle (Noll et al., 2020). The results for *A. timida* differ strikingly from other previously studied species. The clear-cut pattern is also found in other Epiponini like *Apoica* and *Polybia dimidiata* (Noll et al., 2004). Still, it was never found in species with small colonies (a few dozen individuals) such as *Agelaia timida* (Noll et al., 2020). Thus, *A. timida* fits into morphological skew theory, since the species form small colonies with low caste differentiation and nonsterility of workers.

Agelaia timida presents intermediate females, which is exceptional for the genus as it was previously found only in *A. lobipleura* (Richards, 1978), a species that belongs to the same clade as *A. timida* in the phylogeny of the genus (Andena et al., 2024). The occurrence of laying workers in epiponines (intermediates) suggests reproduction may not be entirely the charge of queens. Even though these non-inseminated layers have mainly been found in species with low caste dimorphism, they have also been found in species with caste differences (Noll et al., 2004).

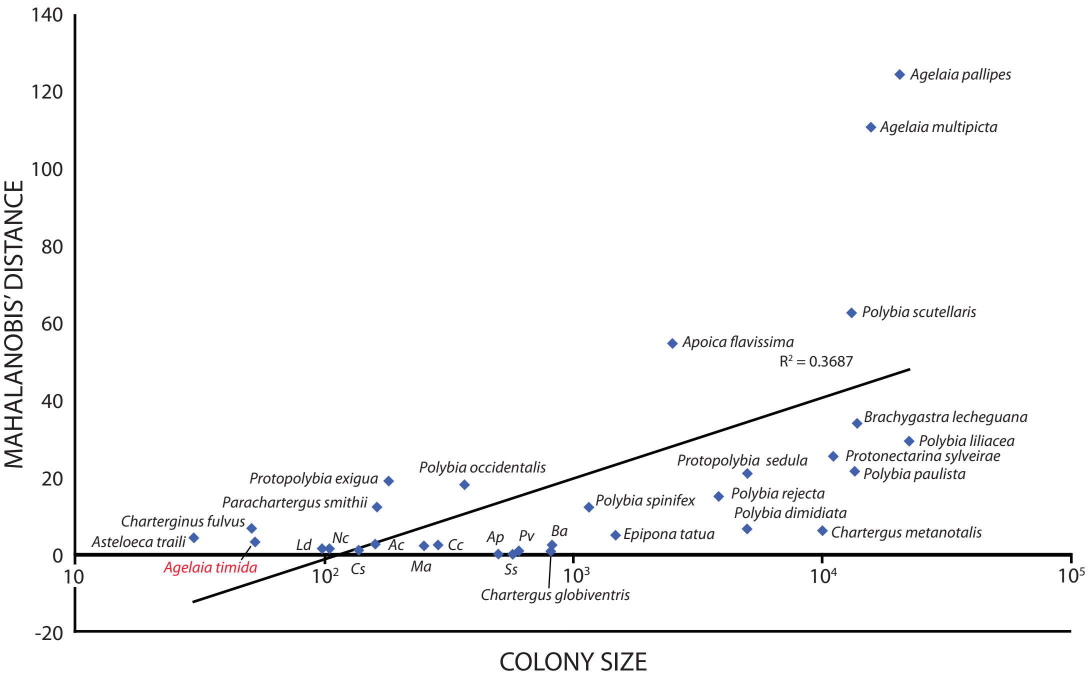

FIGURE 4. Mahalanobis distance values versus colony size among species of Epiponini using discriminant function analysis. Abbreviations: *Ac*, *Agelaia cajennensis*; *Ap*, *Angiopolybia pallens*; *Ba*, *Brachygastra augusti*; *Cc*, *Chartergellus communis*; *Cs*, *Clypearia sulcata*; *Ld*, *Leipomeles dorsata*; *Ma*, *Metapolybia docilis*; *Nc*, *Nectarinella championi*; *Pv*, *Pseudopolybia vespiceps*; *Ss*, *Synoeca surinama*.

The low value of Mahalanobis distances obtained for *A. timida* (3.47), which indicates low differentiation between castes, strongly contrasts with the high values obtained for other *Agelaia* species, such as *A. vicina* (207.15 and 176.7; Baio et al., 1998), *A. pallipes,* and *A. multipicta* (124.67 and 110.99, respectively; Noll et al., 1997a) (fig. 4, table 3). A low value of Mahalanobis distances was also found for other species, such as: *Pseudopolybia vespiceps* (0.99; Shima et al., 1998), *Polybia dimidiata* (6.76; Shima et al., 1996b), *Protopolybia exigua* (4.95, Noll et al., 1996) and *Apoica flavissima* (11.27; Shima et al., 1994).

Richards (1978) in his book *The Social Wasps of the Americas* states that the only *Stelopolybia* (= *Agelaia*) known to make nests with envelopes are *A. areata* (Say) and *A. flavipennis* (Ducke), however, the envelope in these cases are the backs of the cells playing the role of protecting other parts of the comb. Cooper (1986) found and described two nests of *Agelaia* covered with a real envelope, both attached to the underside of leaves. On that occasion he identified the nests as belonging to *A. cajennensis* (F.). Later, Cooper (2000) corrected the identification, saying that in fact those nests were *A. timida* and not *A. cajennensis*.

The combination of less markedly distinct castes, plus the presence of a real envelope in *Agelaia timida* is an interesting aspect for the evolution of *Agelaia*. Considering that *A. timida* is part of the sister clade of all other species of *Agelaia* (Andena et al., 2024), it can

TABLE 3. Mahalanobis distance values for Epiponini species. Colony size and obtained values of Mahalanobis distance for *Agelaia timida* and 30 other species of Epiponini (data from literature).

Species	**Colony size**	**Mahalanobis**	**Reference**
Agelaia multipicta	15600	110.99	Noll et al., 1997a
Agelaia pallipes	20400	124.67	Noll et al., 1997a
Agelaia timida	**53**	**3.47**	
Agelaia cajenensis	160	2.77	Noll, unpub. data
Angiopolybia pallens	500	0.31	Gelin, et al., 2008
Apoica flavissima	2500	54.99	Noll and Zucchi, 2002
Asteloeca traili	30	4.52	Noll et al., 2004
Brachygastra augusti	824	2.56	Baio et al., 2004
Brachygastra lecheguana	13800	34.02	Shima et al., 2000
Chartergellus communis	286	2.65	Mateus et al., 1999
Charterginus fulvus	51	6.95	Noll et al., 2004
Chartergus globiventris	812	1.09	Noll et al., 2004
Chartergus metanotalis	10000	6.34	Noll et al., 2004
Clypearia sulcata	138	1.23	Noll et al., 2004
Epipona tatua	1478	5.16	Noll et al., 2004
Leipomeles dorsata	105	1.67	Noll et al., 2010
Metapolybia docilis	251	2.31	Baio et al., 2003
Nectarinella championi	98	1.68	Noll et al., 2004
Parachartergus smithii	154	8.94	Mateus et al., 1997
Polybia (Cylindroeca) dimidiata	5000	6.76	Shima et al., 1996b
Polybia (Formicicola) rejecta	3838	15.29	Noll et al., 2004
Polybia (Myrapetra) occidentalis	367	18.22	Noll and Zucchi, 2000
Polybia (Myrapetra) paulista	13479	21.6	Noll and Zucchi, 2000
Polybia (Myrapetra) scutellaris	13119	62.77	Noll et al., 1997b
Polybia (Pedothoeca) spinifex	1159	12.32	Noll et al., 2004
Polybia (Polybia) liliacea	22384	29.46	Noll et al., 2004
Protonectarina sylveirae	11071	25.64	Tanaka et al., 2010
Protopolybia exigua	182	19.2	Noll and Zucchi, 2002
Protopolybia sedula	5000	21	Noll and Zucchi, 2002
Pseudopolybia vespiceps	603	0.99	Shima et al., 1998
Synoeca surinama	572	0.29	Noll et al., 2004

be suggested that the characteristics observed in *A. timida* may be plesiomorphic, as we can partially observe in the ground plan of Epiponini, similar to what is found in *Angiopolybia* (Noll et al., 2021). In this scenario, the other clade of *Agelaia* species might have an ancestor that evolved into a very rigid caste system, with clear physiological distinction, large populations, and loss of envelope.

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