



RESEARCH ARTICLE - ANTS

Caste-specific phenotypic plasticity of Asian weaver ants: Revealing the allometric and non-allometric component of female caste system of *Oecophylla smaragdina* (Hymenoptera: Formicidae) by using geometric morphometrics

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Abstract

In eusocial insects, particularly in ants, caste differentiation is extremely complicated when we rely on traditional taxonomy. In most species, the worker caste does not display any distinct morphological characters neither the caste's central division according to their morphological size variations. We used a landmark-based geometric morphometric approach to quantify the morphological characteristics of female caste systems (queen, major and minor worker ant) of *Oecophylla smaragdina*. Our findings suggested that each caste has its unique shape and size. Especially in the worker caste, apart from the size variations, we can use the shape as a prominent tool for distinguishing between them. The *O. smaragdina* exhibits a triphasic allometry pattern. Studying the allometry and non-allometry components of each caste system revealed a highly complex size and shape relationship in the female caste systems. From the allometric and non-allometric analysis, we concluded that the major worker ants showed a closer relationship with the queen than the minor worker ant. This outcome demonstrated that Asian weaver ant exhibits complex shape variations related to size and is correlated to their functional modular characters. This research sheds new light on caste systems' taxonomic uncertainties for eusocial hymenopteran groups, especially ants.

Introduction

The shape is an essential geometrical feature in biological systems. It links genotype with the environment (Kendall, 1977; Bookstein, 1991; Dryden & Mardia, 1998), and it varies according to the size (Adams et al., 2013). Allometry is the statistical relationship between size and shape (Mosimann, 1970). In a more general context, allometries can be understood as a differential change of a quantitative character with variation in overall body size (Seifert, 2008; Yazdi, 2014). Geometric morphometric analyses were used to study the phenotypic plasticity, asymmetry, and allometry of the structure under study (Klingenberg, 2015). Fluctuating asymmetry (FA) is a principal area of interest because it was proved that mate selection and survival rates are affected by the FA of the individual and are closely related to the organism's fitness (Scheib et al., 1999).

The Geometric morphometric characterization of the ant caste system is not well studied. Several researchers are focused on the evolution of eusocial insects with their division of labor related to the functional morphological adaptations (Oster & Wilson, 1978; Rajkumar et al., 2012; Molet et al., 2012; Powell, 2016; Tribble & Kronauer, 2017; Wills et al., 2018; Powell et al., 2020). This paper considers the caste-specific phenotypic plasticity of the Asian weaver ant (*Oecophylla smaragdina*). They are obligate arboreal forms found in tropical Asia and Australia (Holldobler, 1983; Fiedler & Maschwitz 1989; Schluns et al., 2009; Sullivan, 2012). The individuals show a division of labor, and the caste system is well defined with a heavy-bodied queen, males, and sterile female workers. *Oecophylla* workers are dimorphic (major and minor), which shows a difference in size and function.



Major workers are 8-10 mm long, perform outdoor tasks such as foraging and defense, whereas minor workers are 4-5 mm long, and they take care of the brood (Holldobler & Wilson, 1977). Minor workers live longer than majors (Chapuisat & Keller, 2002). Queen is generally 20-25 mm long and normally greenish-brown in color and shows high territoriality (Langthasa et al., 2017).

It has already been established that *O. smaragdina* shows unusual triphasic allometry (i.e., the continuous form of the queen to the dimorphic distribution of the worker caste). Furthermore, this species' peculiar allometry characteristic feature can be used for a valuable model system to understand each caste's allometric components (Wilson, 1953; Crozier et al., 2010; Wills et al., 2018). This is the first investigation report related to the geometric morphometric analysis of Asian weaver ant female caste system (queen, major and minor worker ants). We address the following questions in this study: (1) Determining the size and shape difference between the female caste system of Asian weaver ant, in particular, in the worker caste are there differences in size only between the major and minor worker ants? Are there variations in shape? (2) Understanding the caste-specific size and shape relationship; (3) Analysing the allometric and non-allometric components of queen, major and minor worker caste.

Materials and methods

Data sets

The test organisms' Asian weaver ant, *Oecophylla smaragdina* (Fabricius, 1775) (Hymenoptera: Formicidae), were collected from Calicut University campus, Kerala, India (11°12'69.59" N and 75°89'23.33" E). After anesthetization, the individuals of a queen, major and minor ants were sorted out. The ants were mounted on a clean slide by using glycerine and ensure minimum contortion in orientation. The whole body's dorsal view was photographed using Canon EOS 5D Mark IV Camera and MP E 65 (1-5x) f-16, ISO 1000 Canon lens, Japan (all specimens are arranged the same plane for better statistical analysis). Based on classical morphological taxonomy, 31 homologous landmarks were marked on the organism's dorsal side (Bingham, 1903) (Fig 1A).

Data analysis: correlation between shape and tangent space

Before performing different analyses, the correlation between the Procrustes and tangent distances was calculated using tpsSmall V 1.34 (Rohlf, 2003). In this section, the raw data were transformed into Euclidean distances tangent space via full Procrustes superimposition, which is crucial in GM analysis, especially in articulated structure (Kendall, 1977; Bookstein, 1997; Rohlf, 1999). By calculating the regression slope and the correlation coefficient between the Procrustes distances in the shape space and the Euclidean distances in the tangent space, it is possible to determine whether the magnitude of the variance in the data set is small enough for further statistical analysis (Rohlf, 2015; Katzke et al., 2018).

Measurement of landmark error

To avoid an error in the landmarking procedure, a sample of individuals was digitalized twice. A Procrustes ANOVA was conducted to determine whether the mean square (MS) values for the individuals were lower than the error (Fruciano, 2016; Klingenberg, 2016).

Geometric morphometric analysis

2D images of female castes of the weaver ant (queen $n = 9$, major $n = 221$, and minor $n = 186$) were converted into TPS file format (using tpsUtil V1.68) for registering landmarks (using tpsDig V2.26) (Rohlf, 2015). The allometric and non-allometric shape and size analysis of major, minor, and queen caste was carried out according to Debat et al. (2013) and Klingenberg (2016). All geometric morphometric analyses were done in the Morpho J v 1.07a tool 2016 (Klingenberg, 2011). The canonical multivariate analysis (CVA) was also performed to characterize the covariation between different castes (Klingenberg, 2010).

Relationship between size and shape

The multivariate regression analysis was used to determine the relationship between each caste's size and shape: we fixed size as an independent variable, and shape selected as a dependent variable with 10,000 permutational analyses was used to estimate their significance level (Klingenberg, 2016).

Results

Shape and tangent space

The variation of each specimen in shape space was perfectly correlated with tangent space for all morphological aspects. The regression slope is very close to 1.0 in all caste (major = 0.999612; minor = 0.986228; queen = 0.986228) and presence of high correlation coefficient (major = 1.000; minor = 0.999962; queen = 0.999962). It indicated that shape changes in each caste are accurately captured for subsequent statistical analysis.

Caste specific size & shape analysis

Marginally significant landmarking errors can be observed in our datasets. They indicate the heterogeneous population nature of the caste. All three different castes within the group did not show any statistically significant size variations (major $F_{0.18}$; $p = 1.00$, minor $F_{0.93}$; $p = 0.64$, and queen $F_{0.89}$; $p = 0.57$). The significant shape variations were observed only in worker caste ($p < 0.001$), and the fluctuation asymmetry (FA) was prominently expressed in all castes (Table 1). The means of centroid size were significantly different between all castes ($p < 0.001$); the queen is significantly bigger than major and minor worker ants (Fig 1B). Furthermore, significant shape differences

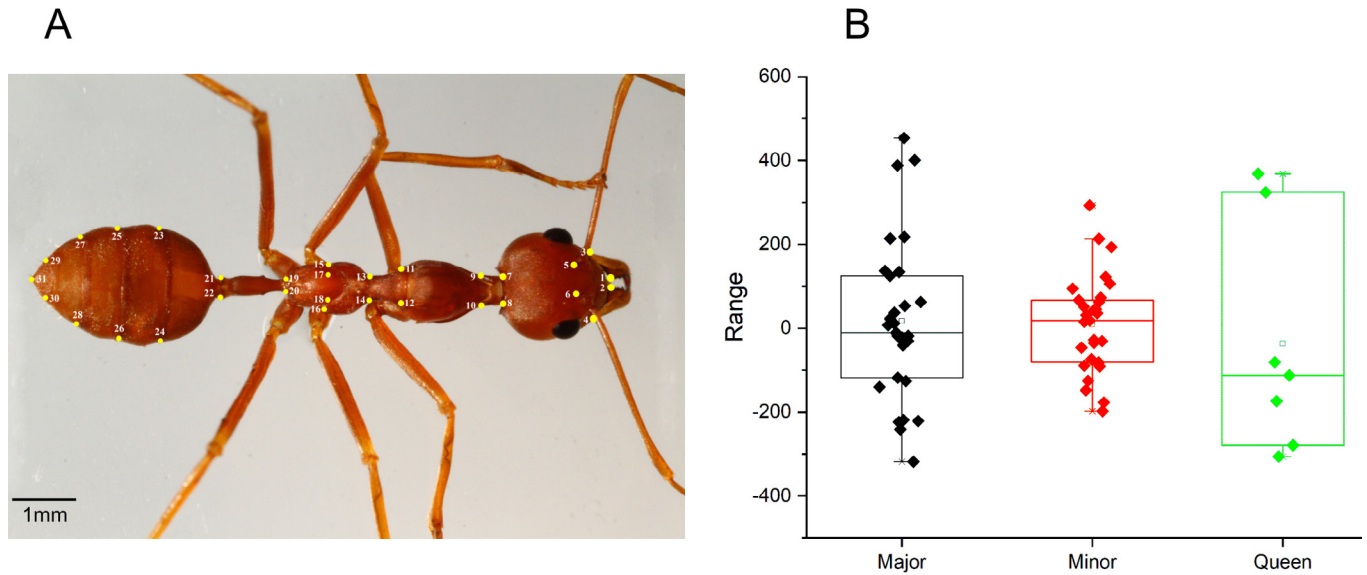


Fig 1. (A) Selected landmarks – represented in worker ant. (B) Centroid size range of major, minor and queen (coloured diamond box indicates each PCs' centroid size).

were observed between the major and minor worker castes ($F_{1,29}$; $p < 0.0001$). Therefore, we proved our hypothesis that, apart from the size differences, the worker castes showed significant shape differences between them.

Relationship between size and shape

In the multivariate regression analysis, size is fixed as the independent variable and shape as the dependent variable. Statistically significant caste specific size-related shape was

observed in major (22.139% $p < 0.0001$), minor (17.397%, $p < 0.0001$) and queen (32.039%, $p = 0.045$).

Visualization of allometric variations

The patterns of variation in shape can be explored by principal component analysis (PCA). A set of 31 landmarks was digitalized in the female caste system's entire dorsal side (*O. smaragdina*). A total of 29 PCs presents in the worker castes and seven PCs present in the queen.

Table 1. The centroid size ANOVA and Procrustes shape analysis of the female cast of *O. smaragdina*.

Analysis	EFFECT	SS	MS	DF	F	P (param.)
Major						
Centroid size	Individual	287.096734	2.4966493	115	0.18	1.0000
	Error	1493.315635	14.222054			
Shape	Individual	0.11840121	0.0000355026	3335	1.31	<0.0001
	Side	0.01133501	0.0003908624	29	14.39	<0.0001
	Ind*side	0.09056015	0.0000271545	3335	6.85	<0.0001
	Error	0.0214275	0.0000039643			
Minor						
Centroid size	Individual	16726543.6950	174234.8301	96	0.93	0.6407
	Error	16893283.8310	187703.1536			
Shape	Individual	0.10409733	0.0000373913	2784	1.12	0.0018
	Side	0.00270174	0.0000931634	29	2.78	<0.0001
	Ind*side	0.09324380	0.0000334927	2784	9.57	<0.0001
	Error	0.01827197	0.000035004			
Queen						
Centroid size	Individual	36.288595	7.257719	5	0.89	0.5776
	Error	24.494184	8.164728			
Shape	Individual	0.00452437	0.0000312025	145	0.20	1.000
	Side	0.01395312	0.0004811420	29	3.11	<0.0001
	Ind*side	0.02242245	0.0001546386	145	2.97	<0.0001
	Error	0.00906221	0.0000520816			

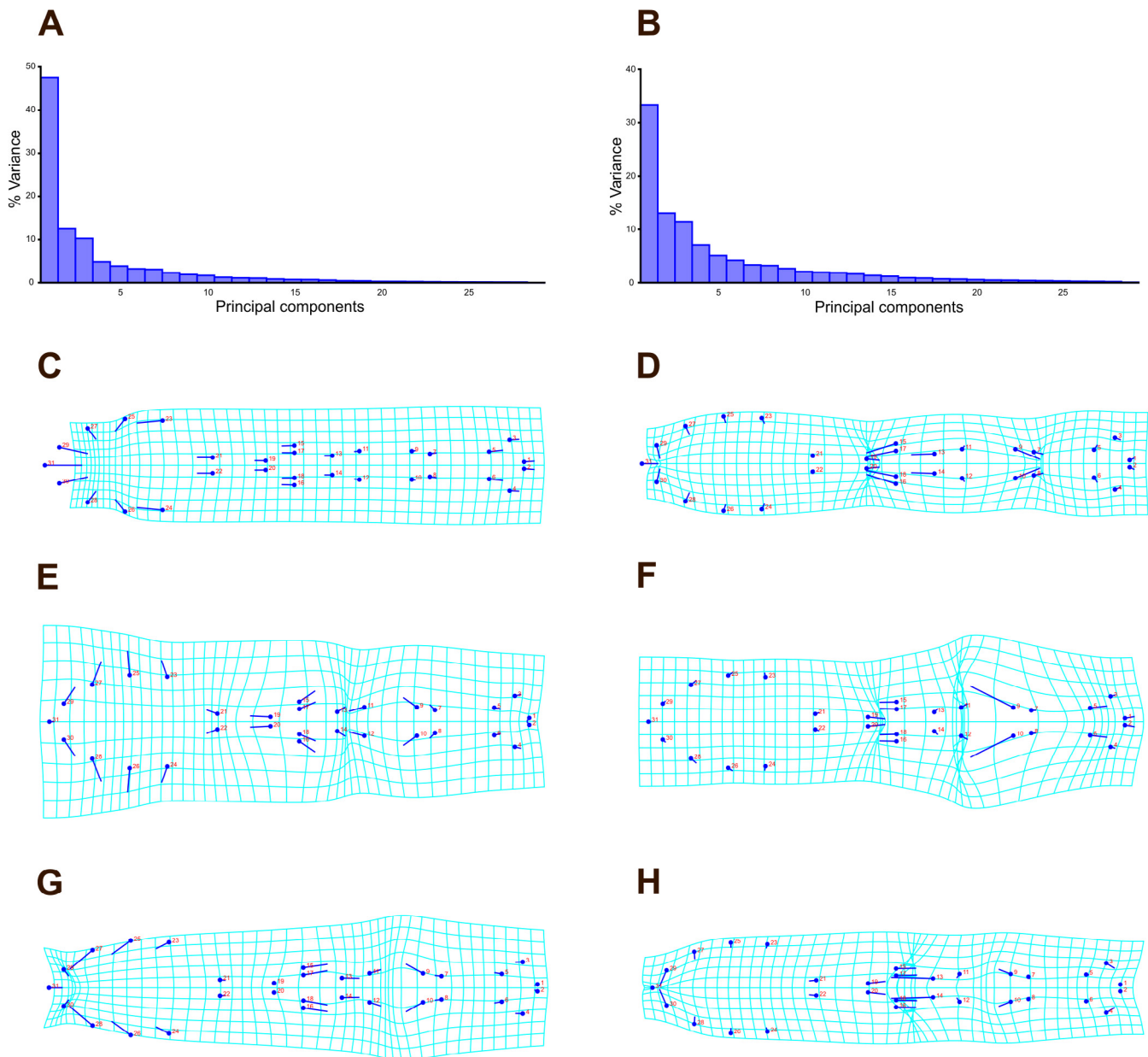


Fig 2. Major worker ant (A) Percentage of variance in allometric analysis; (B) Percentage of variance in non-allometric; C, E & G: PC1, PC2 and PC3 of allometric analysis; D, F & H: PC1, PC2 and PC3 of non-allometric analysis

Major worker ant: The cumulative percentage of PCA of major worker ants was 70.293% (PC1 = 47.535%, PC2 = 12.480%, PC3 = 10.278%) (Fig 2A). Shape analysis through PCA is visualized by the distortion grid. In PC1 (Fig 2C), high level of shape variations were observed in the abdomen regions followed by the thoracic region and head. A significantly narrowed construction of thoracic areas was observed in PC1. The striking feature in PC1 is the widening of the head's anterior region and the lengthening of the petiolar region. In PC2 (Fig 2E), the highly variable part is the metathorax, followed by the abdomen, the prothorax, and the head. The abdomen showed striking shape variations, such as widening of abdomen regions (the highly influenced landmarks in the abdomen regions are 23-30). The landmarks no. 9 and

20 delivered the maximum variations, i.e., widening of the thoracic regions. The elongated slender body is the major variation found in PC3 (Fig 2G) with oval-shaped thoracic regions. By analyzing the first three PCs, the expansion from mandibular areas and thoracic and well-constructed abdomen are the main characteristic features observed in major worker ants.

Minor worker ant: The cumulative percentage of the first three principal components of minor worker ants was 58.212 % (PC1 = 32.326%, PC2 = 13.773%, PC3 = 7.113%) (Fig 3A). In PC1 (Fig 3C), the maximum deviation is shown in the abdomen regions, thoracic region, and head. The last four abdominal segments showed the highest variability due to the distortion of 23-31 landmarks. All landmarks in

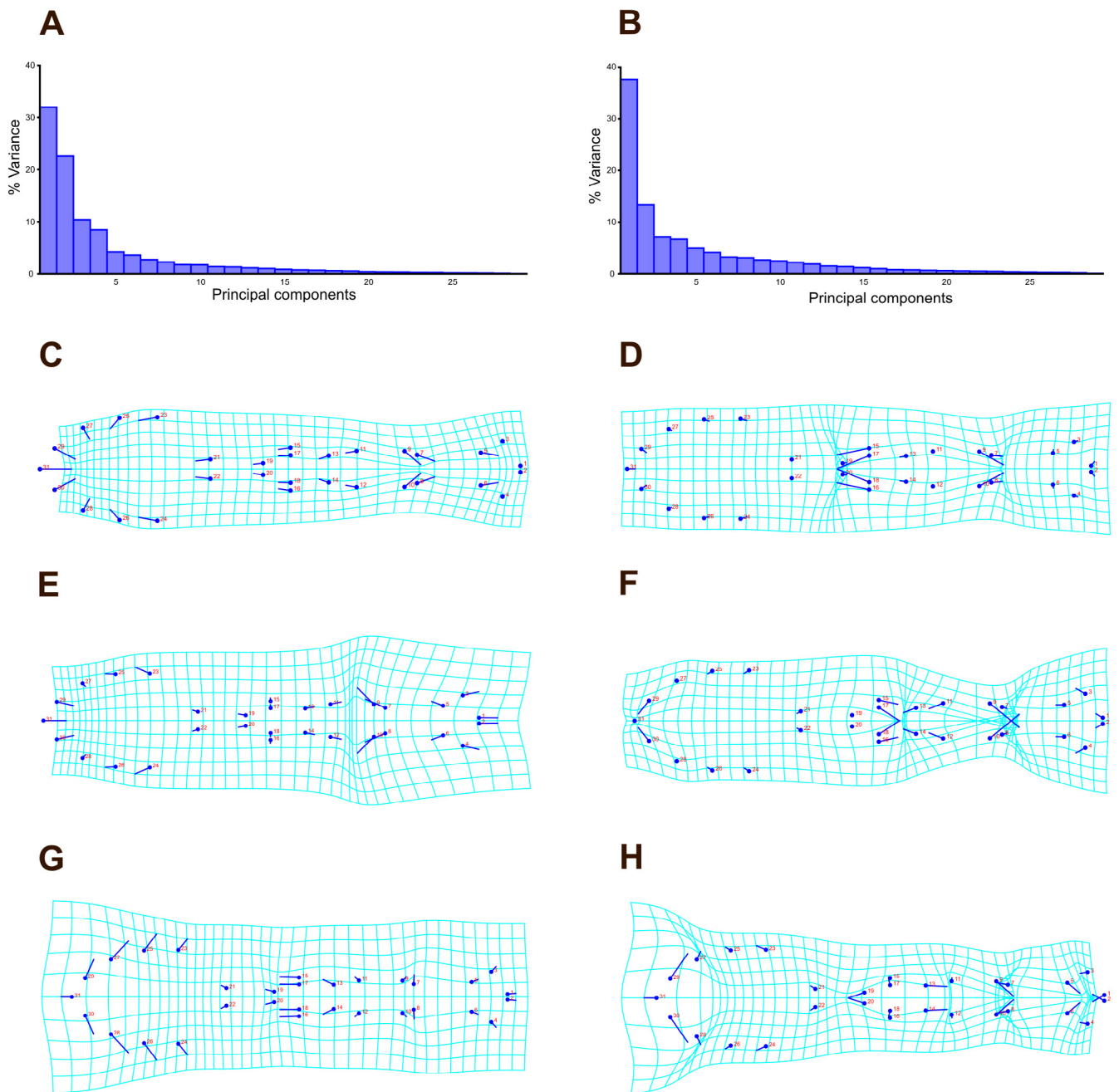


Fig 3. Minor worker ant (A) Percentage of variance in allometric analysis; (B) Percentage of variance in non-allometric; C, E & G: PC1, PC2 and PC3 of allometric analysis; D, F & H: PC1, PC2 and PC3 of non-allometric analysis.

the abdomen region were focused on the inward direction. Landmarks 5-8 showed a high level of deviations in the head region compared to other landmarks. In PC2 (Fig 3E), the posterior part of the head and anterior part of the thorax showed the maximum variations. Widening of the prothorax and anterior part of the abdomen is the major characteristic variation observed in PC2. Widening of the head, prothorax, and abdomen are the major distinguishing features observed in PC3 (Fig 3G). The widened abdomen and reduced head with the well-expanded thoracic region are the most typical variations found in minor worker ants.

Queen: The first two PCs covered around 87.641 % of the variations (PC1 71.504 % and PC2 16.137 %) (Fig 4A). The highly complex structure of the queen exhibits varying morphological size and shape variations. All parts showed different kinds of variations, widening of prothorax and abdomen, whereas the construction of meso and metathorax region is the striking features present in PC1 (Fig 4C) of a queen. The contradictory variations were observed in PC2 (Fig 4E) because the abdomen region is more or less similar to normal conditions, not showing too many variations. Nonetheless, the reduced metathoracic region is the striking

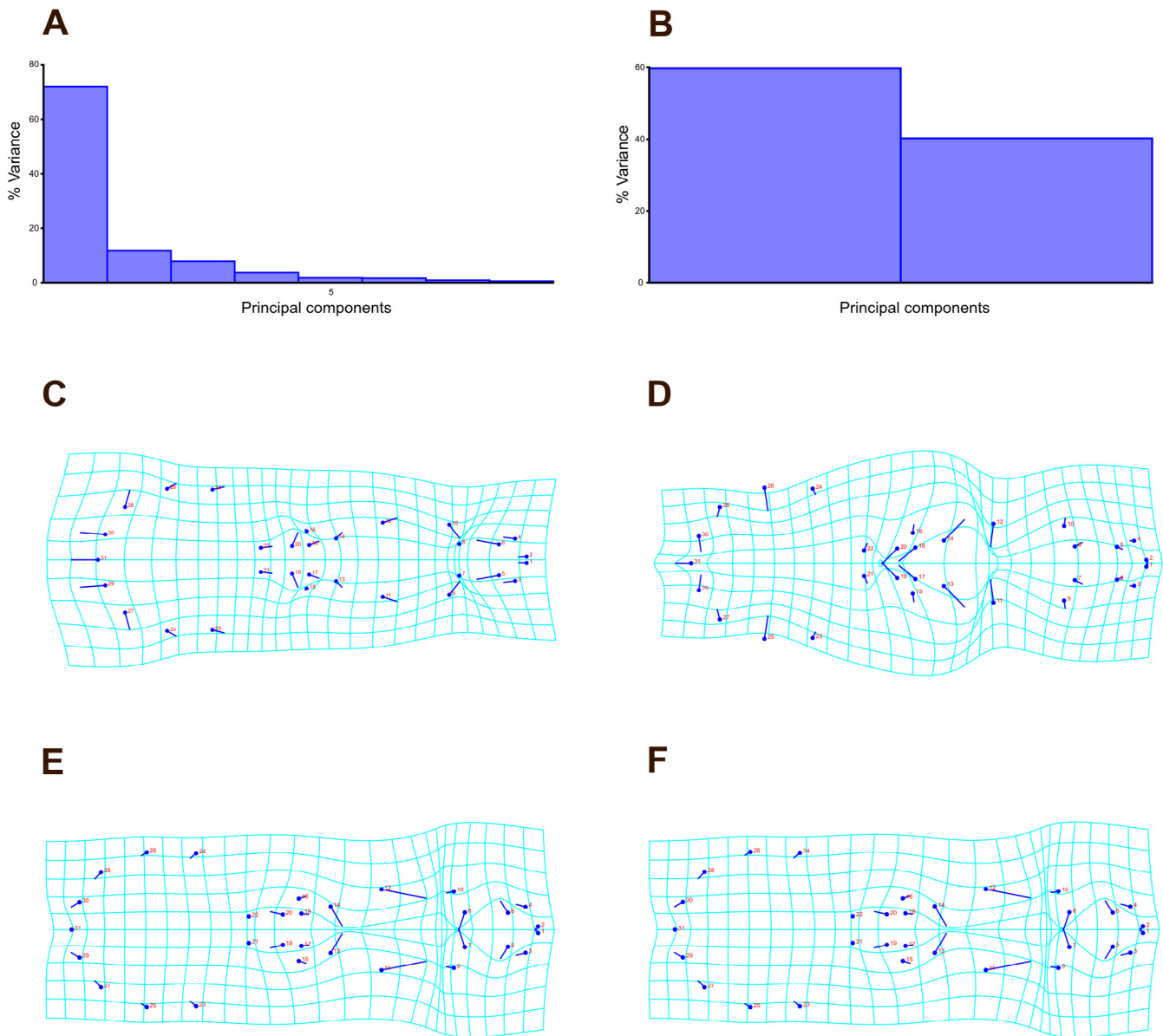


Fig 4. Queen (A) Percentage of variance in allometric analysis; (B) Percentage of variance in non-allometric; C & E: PC1 and PC2 of allometric analysis; D & F: PC1 and PC2 of non-allometric analysis.

feature of PC2, besides widened prothorax regions with reduced head. The overall PC analysis proved that well-expanded abdomen, pro, and mesothoracic regions with a reduced head are the major characteristic variations expressed in the queen.

Visualization of non-allometric variations

By removing the allometric impact on the female caste showed a significant level of variations. This kind of analysis can be used for assaying the shape variations without the influences of external factors, such as age, sex, caste etc.

Major worker ants: a total of three PCs covered 57.806 % of variations (PC1 = 33.341 %, PC2= 13.021 %, PC3= 11.445 %) (Fig 2B). In PC1 (Fig 2D), most variations were observed in thoracic regions and followed by abdomen

and head. Elongation of thoracic regions is the major feature found in PC1. In the abdomen, all landmarks focused on inward movements; they indicated the size reduction. Well constricted thoracic regions and less expanded abdomen, and the elongated head region are the major striking features observed in PC2 (Fig 2F). In PC3 (Fig 2H), the highly variable region is the metathoracic, followed by the abdomen last segments and anterior part of the head (mandibular basal regions). Among the three PCs, the 2nd PC showed only expansion of abdomen regions, PC1 and PC3 almost share similar characteristic features, but the level of variations covering range is different.

Minor worker ants: around 58.071 % of variations are covered by the first three PCs. PC1 covered 37.622% of variations, followed by PC2 (13.298%) and PC3 (7.150%) (Fig 3B). PC1 (Fig 3D) covered the major variations in the

thoracic region's anterior and posterior parts and was followed by the abdomen and head. In PC2 (Fig 3F), the most visible variations are well-constricted and shortened thoracic regions plus an elongated abdomen. A well expanded and highly variable abdomen was observed in PC3 (Fig 3H), followed by thorax and head. Elongated thorax, widened abdomen, and a small head is the major striking variations were observed in PC3.

Queen: Only two PCs were found in this analysis, with 59.945% of variations covered by PC1 and 40.055% of variations covered by PC2 (Fig 4B). The PC1 (Fig 4D) covered the major variations in the thoracic region, followed by the abdomen. Only a small number of variations was observed in the head regions. The small head region is the major characteristic feature observed in PC1. Expansion of the thoracic region and shortening of the petiolar region with a well-constricted abdomen were also observed in PC1. All landmarks in the abdomen region showed inward movements, except landmark number 31. As for PC2 (Fig 4F), a high level

of variations was observed in the prothoracic regions. Also, we observed the elongation of the abdomen regions with a shortening of the thoracic region.

Canonical variate analysis

The discriminant analysis (CV1 =81.678% and CV2 = 18.322%) proved that each caste of weaver ants showed unique morphological characteristics because such features were distributed in a distinct trait-based morphospace (Fig 5A). The queen is entirely shifted from the worker caste group, and CV2 positively influences it. Major and minor worker ants are close to each other; this might be due to sharing similar trait characters. The contradictory outcome was observed in Hierarchical cluster dendrogram analysis (based on Mahalanobis distance between each caste) (Fig 5B) of the female worker caste. Surprisingly, we found that major caste traits showed a closer relationship with the queen than with the minor worker.

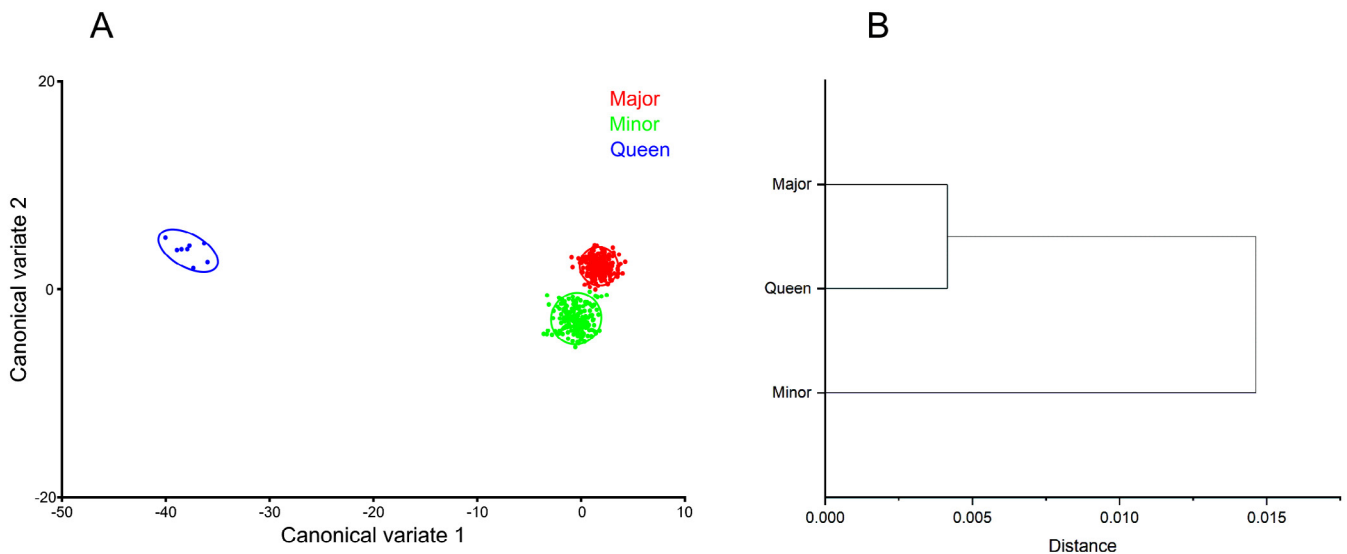


Fig 5. (A) Canonical variate analysis of queen, major and minor worker ants (B) Hierarchical cluster dendrogram analysis of female caste of Asian weaver ant using Mahalanobis distance between each caste.

Discussion

The quantification of shape is an integral part of biological research in recent years. Geometric morphometrics can be used as a tool in the identification of individuals beyond the species level by providing more detailed information on minute morphological differences between individuals of a population or different populations of the same species. Our study quantified the morphological variations in different castes of *O. smaragdina* (queen, major and minor). The study results have shown a relationship between morphological variation and size-related labor division in *O. smaragdina*. The Procrustes shape ANOVA analysis of the female caste system (major, minor, and queen) showed significant shape and size variations along with FA. We proved that each caste has its unique shape and size features; especially in the worker caste,

apart from the size variations, they also exhibit statistically significant shape variations. In our selected population, worker caste exhibits a highly heterogenous population nature than the queen. Some studies suggested that the worker caste has functionally unspecialized intermediate-size workers. These workers might be the reason for FA's presence, landmark error in our data, and the data's heterogenous nature. They convey the disparity in individuals' or groups' genetic and environmental stresses during the development phase (Joseph & Kotiaho, 2001).

Geometric morphometrics allows us to observe the allometries of a particular shape component that might not be easily identified through a traditional morphometric analysis (Seifert, 1988; Yazdi, 2014). The allometric and non-allometric PCA analysis of the *O. smaragdina* female caste revealed the existence of a caste-specific shape variation. In major worker

ants, the variation is more prominent in the abdominal regions and followed by the head. In minor worker ants, the thorax, abdominal region, and head are the core parts more susceptible to variation. The queen also showed a crucial variation in the abdomen and thoracic regions. The head exhibited a remarkably reduced size. After removing the allometric factors, the complex phenotypic morphological variations were observed in all caste. Surprisingly, similar shape variations (supporting our findings) were also observed in the allometries analysis of the fire ant's worker caste, *Solenopsis invicta* (Tschinkel et al., 2003). It is difficult to understand each caste's structural and functional modifications under allometric and non-allometric conditions. Based on the allometric and non-allometric analysis, we can confirm that the queen thoracic and abdomen architecture is very complicated, and it may facilitate the modular functional organization of each part. The well-developed abdomen indicated their reproductive functions and the thoracic architecture complexity indicated as their developed wing muscles for the flight mechanisms. Based on the PCs results (allometric and non-allometric), the infrequent size variations were observed in the weaver ant caste system, especially in the worker caste. The finding of this study suggests that the body size of worker ant will evolve more rapidly than the shape of the body (Stanley, 1979; Stanley & Yang, 1987; Clyde & Gingerich, 1994; Hunt, 2007; Wood et al., 2007; Dzeverin, 2008).

Based on a regression analysis, statistically meaningful findings were observed in all caste. The critical factor behind the inconsistent expression and quantification of allometric residues is the individuals' various sizes and shapes (Drake & Klingenberg, 2008; Klingenberg, 2016). Small differences in nutrients and food resources and other abiotic and biotic factors actively play a vital role in phenotypical plasticity (Huang & Yang, 1987; Way & Khoo, 1992; Peng & Christian, 2004; Rajkumar et al., 2012; Powell, 2016; Tribble & Kronauer, 2017; Willis et al., 2018; Powell et al., 2020); currently no active records available related to the phenotypic plasticity of eusocial insects related to environmental conditions. Future studies could explore the relationship between environmental conditions (including diet) during ants' life history and the resulting phenotypic plasticity, measured by Geometric morphometrics. This heterogeneous nature in the caste system's shape and size will alter the expression and significance level of regression analysis. Only a few morphometric studies were conducted in formicide groups. The geometric morphometric analysis of selected worker ants of *Diacamma rugosum* proved that age and size-related shape variations are expressed in castes, and it is related to their task partitioning (Manting et al., 2013). Similar kinds of works were done in mandibular shape analysis of major and minor worker ant of *Camponotus* species. The discriminant analysis indicated that significant shape variations observed in the left and right mandibles of major and minor worker ants might be due to their function in the nest (Bacaraman et al., 2016).

The ants acquired a wide range of adaptation through their morphological shape modulation based on their functions. The different kinds of morphological variations and their expression indicated their origin and expression of dynamic functional phenotypic integration of body parts. The morphological integrations are not necessarily in the entire body but are more concentrated in various of the internally deeply integrated components although independent of other complexes known as modules (Klingenberg & Zaklan, 2000; Klingenberg, 2008). Based on their functional adaptations and the shape variations, the mandibular region of the major workers ant behaves as modules as well the thoracic architecture of minor and queen showed modular organization as separate subsets like prothorax, mesothorax, and metathorax (in the allometric and non-allometric analysis, each region or subsets or modules are independently expressed). Keller et al. (2014) analyzed workers' and queens' thorax morphology using the linear morphometrics method. They observed unique skeleton muscular modifications in workers that, in turn, increase the power and flexibility of head-thorax articulation. Their result reveals that ants invest in the relative size of thorax segments according to their tasks.

CVA proved that each caste exists in a distinct trait morphospace, but the contradictory outcome was observed in hierarchical cluster dendrogram analysis using Mahalanobis distance between each caste. Major worker ants showed a close relationship with queen compared to minor; in normal case, the size distribution is bimodal, one is comprised of worker like individuals while the other of queen like individuals (Wilson, 1953; Wheeler, 1991; Fjerdingstad & Crozier, 2006). We hypothesised that; in *O. smaragdina* major worker ant traits are sequentially transformed to the queen like traits during the evolutionary time period. Because, in the allometric and non-allometric PCs analysis, both the major worker ant and queen exhibit a similar set of shape variations, i.e., most of the variations were observed in the abdomen and in the head. According to Brian (1955) and Londe et al. (2015), worker to the queen like phenotypic trait progress existed in ant's caste system; the intercaste progress from slightly larger than workers to slightly smaller than queens. According to Tribble and Kronauer, (2017), species gain or lose caste throughout their evolutionary time either by altering the size-frequency distribution or adjusting the tissue growth and size relationship. More studies are required to resolve the existence of intercaste in Asian weaver ants and its morpho-functional modifications. We would like to mention that we are well aware that our study is focused on articulated structures; at present, we do not adopt any statistical method for eliminating the effect of arbitrary rotation of the articulated structures (see Adams, 1999). But we maintained that all specimens are arranged in the same plane for better statistical analysis and assess the correlation between each specimen's shape and tangent space. Based on this analysis, we proved that our data perfectly captured each specimen's entire shape and size for the better statistical analysis.

Some studies address the characteristic allometric feature of worker caste based on linear measurements. In most of the ant species (*Cataglyphis niger*, *Solenopsis invicta*, *Myrmica scabrinodis* and *M. vandelii*) allometry characterization was set from the mature colony (Nowbahari et al., 2000; Tschinkel et al., 2003; Yazdi, 2014). In order to analyze the functional related structural variations of each caste, initially we need to address the size-related shape variations of ants related colony size (Nowbahari et al., 2000). All the above results lead to a common conclusion is that shape variation can be used as a tool in identifying the different individuals of the same species/caste, especially in the morphologically similar worker caste. And this variation is related to the functional difference of the individuals (Peeters & Ito, 2001; Molet et al., 2012; Tribble & Kronauer, 2017; Wills et al., 2018). Shape variation may be interpreted as a change occurring during the evolutive history of taxa. In this way, the geometric morphometric analysis provides information that may be used to obtain evidence of similarity among taxa/population and may be useful in testing hypotheses related to ecology, systematics and evolution (Rohlf & Marcus, 1993; Premoli, 1996). This kind of analysis (allometric and non-allometric) helps to quantify and visualize morphological variation between species (Alibert et al., 2001). The natural selection response well supports the complex shape variations and their phenotypic plasticity, and it helps the evolutionary stability and the selective divergence of an organism. This kind of natural selection responses are the major reason behind the successful colonization, adaptations, and divergence of an organism (Anand & Shibu Vardhanan, 2020).

Conclusion

Our study quantifies the main morphological variations of the *O. smaragdina* female caste system (major, minor worker ants, and queen) using geometric morphometrics. We conclude that a significant caste-specific size and shape exist in each female caste of weaver ants with fluctuating asymmetry and allometry. PCs analysis with and without allometry showed significant shape variations. Among the female caste, the queen showed significantly different shape complexity features compared to the worker caste. And the queen doesn't show any significant shape variations within the group because the phenotypic complexity of the queen shape is evolutionary and functionally highly conserved and led to modular phenotypic integration. The existence of allometry acts as an integrated unit between the subsets/modules. This study proves that landmark-based geometric morphometrics is a useful tool for determining the morphological variation in the eusocial insect's caste system (especially in ants) and can be used for correlating with their functions. The shape variations have a decisive role in the taxonomy, evolution, functional adaptation and organisms' developmental instability.

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Authors' contribution

Conceptualization: YSV, KVM, & PPA
 Methodology: YSV, PPA, & SS
 Software: YSV & SS
 Validation: KVM, PPA, SS, YSV, EM
 Formal analysis: PPA, SS, EM & YSV
 Investigation: KVM & PPA
 Resources: KVM
 Data curation: KVM, PPA, & YSV
 Writing: PPA & YSV
 Visualization: YSV & PPA
 Supervision: YSV
 Project administration: SS & YSV
 Funding acquisition: YSV
 All authors reviewed the manuscript.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Disclosure statement

The authors declare that they have no competing interests.

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