



Caste-specific quantitative genetics and phylogenetic signal analysis revealed the morphological adaptation of Asian weaver ant, *Oecophylla smaragdina* (Hymenoptera, Formicidae)

P.P. Anand

Biochemistry and Toxicology Division, Department of Zoology, University of Calicut, Kerala, India 673 635.

✉ anandpp633@gmail.com

 <https://orcid.org/0000-0002-2400-2823>

K.V. Mahima

Biochemistry and Toxicology Division, Department of Zoology, University of Calicut, Kerala, India 673 635.

✉ mahima23596@gmail.com

 <https://orcid.org/0000-0002-5847-815X>

Y. Shibu Vardhanan

Biochemistry and Toxicology Division, Department of Zoology, University of Calicut, Kerala, India 673 635.

✉ svardhanan@gmail.com

 <https://orcid.org/0000-0001-9820-886X>

ABSTRACT. Insect caste development and their morphological divergence are not yet studied well, especially in ants. However, the role of developmental and genetic integration in evolution is contentious. In our study, we tried to reveal the quantitative genetics selection responses, phylogenetic signal, and evolutionary origin of weaver ant female castes (queen, major and minor). The widening and lengthening of the head region, as well as the well-developed mandibular process, are the major heritable characteristics found in the major worker ants. We hypothesized that these conserved and heritable characteristics may help the major worker ants for defense, foraging purposes and other nest-building function aspects. However, in the case of minor worker, small heads and the reduced mandibular process are the more heritable characteristics. Compared to worker ants, in queen, the highly heritable and conserved morphological character is well-developed thoracic regions and large-sized abdomen. It is interesting to note that there is no detectable phylogenetic signal across the female cast of the Asian weaver ants, which suggests that the caste development and morphological divergence are environmentally modulated not evolutionary conserved. From this study, we concluded that caste-specific morphological shape and size are highly conserved traits and these traits are modulated by their niche preferences.

Key words: Geometric morphometrics, phylogenetic signal, heritable characteristics, divergence, weaver ant, caste.

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INTRODUCTION

Weaver ants of the genus *Oecophylla* are among the most successful tropical ants. Currently, there are two recognized species of the genus, *O. longinoda* with eight subspecies and *O. smaragdina* with six subspecies (Bolton et al., 2007). The *Oecophylla* sp., the intermediate-size worker ant, is established initially, and two distinct castes (major and minor) appear later (Cole & Jones, 1948). The castes show a

Corresponding authors: Anand, P.P. (anandpp633@gmail.com) & Shibu Vardhanan, Y. (svardhanan@gmail.com)

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highly polymorphic nature with unusual triphasic allometry. So, *O. smaragdina* could be used as a valuable model system to characterize the allometry changes from a continuous (queen) to a dimorphic distribution of worker castes (major and minor). The eusocial colonization shows a distinct division of labour in ant's caste system with major (outdoor tasks-foraging, defense), and minor (staying inside the nest-performing the brood maintenance) workers and queen (to produce offspring) (Konishi & Ito, 1973; Holldobler & Wilson, 1977). Structurally the weaver ants exist in external bilateral symmetry because the same anatomical parts are repeated on the left and right sides. The variation in repeated parts indicated as their fluctuating asymmetry (FA) has been widely used in evolutionary biology research (Moller & Swaddle, 1997; Klingenberg, 2003 & 2010). FA can be used to measure the developmental instability, environmental stress, hybridization, or fitness (such as reproduction, survivorship, behaviour, and physiology) of an organism (Klingenberg, 2003), and also, it expresses the developmental origin of functional morphological integration (Klingenberg, 2003; Klingenberg et al., 2010).

Several individuals who vary in their allometric coefficients can be characterized as castes in ants (i.e., changing slope when two measurements regress). It follows that individuals of various sizes also vary in allometry, but these various groups do not have a particular functional role in the colony. That is why the body size and caste-associated phenotypes are not linear. In comparison, individuals can have significant differences in size and function but not in allometry. The ants have a phenotypical space ranging from worker-like to queen-like. In regions of this space that are occupied by any given species, there is some versatility. Often identifying these regions as separated castes may be useful, while in other cases considering inhabited areas as a continuum may be more appropriate (Londe et al., 2015; Tribble & Kronauer, 2017). The fundamental principle of quantitative genetics focused primarily on the aggregate effect of all segregate loci that influence on the symmetrical body shape of queen, major and minor worker ants. Inheritance of shape is generally multidimensional. Through natural selection, the evolution of morphological structures relies on the availability of genetic diversities for the design. The selection mechanism is primarily determined by the genetic and phenotypic variability dynamics in the multidimensional structures such as shape, as they are represented by the additive genetic and phenotypic covariance matrices (Lande, 1979; Cheverud, 1984). The assessment of covariance matrices has, therefore, long been fundamental to quantitative developmental genetics (Rohlf, 1997; Lynch & Walsh, 1998). Here, we illustrate the quantitative genetic shape and size selection response of the Asian weaver ant female caste system (queen, major and minor worker ants) and measure the magnitude of the morphological shape inheritance of each caste. The quantitative genetic evolutionary analysis helps to explain the speciation and diversification of the *O. smaragdina* female caste.

MATERIAL AND METHODS

Data sets. *Oecophylla smaragdina* (Asian weaver ant, Hymenoptera, Formicidae) major, minor worker ants, and queen (female caste system) were collected from Calicut University campus (11.13.40° N and 75.89.52° E), Kerala, India. The collected specimens were anaesthetized and categorized as major (n = 108) and minor (n = 93) worker and queen (n = 9) based on their size variations and also morphological taxonomy features (Mahima et al., 2021). According to morphological taxonomy, the homologous taxonomic features of major and minor workers are precisely similar, the minor worker ants were slightly smaller in size (Bingham, 1903). Photographic documentation of specimens was obtained by using Canon EOS 5D Camera and MP-E 65 (1–5×) (Canon® lens, Japan); all specimens are arranged into the same plane to avoid the impact of arbitrary rotation of articulated structure (Mahima et al., 2021; Karthika et al., 2021; Anand et al., 2022).

Geometric morphometric analysis. To explore and quantify morphological variation, the dorsal side of the queen, major and minor worker ants were analyzed and 32 homologous landmarks were obtained (Fig. 1) (Mahima et al., 2021). 2D images were converted for landmark extraction using tpsUtility v. 1.78 and landmarking was done in tpsDig2 v. 2.31 (Rohlf, 2015). The MorphoJ v. 1.07a software was used for

landmark-based geometric morphometric analysis (Klingenberg, 2011). Landmark configurations were superimposed using Generalized Procrustes Analysis (GPA). GPA involves transformations, and superimpositions in the data matrix from individuals, including translation, rotation, isotropic rescheduling, providing an alignment that allows for comparison of the optimized shape from specimens in which the mean generates a consensus matrix (Klingenberg, 2011).

Quantitative genetic analysis. A nested MANCOVA was used to estimate quantitative genetic parameters for the symmetric portion of forms (Begin & Rohlf, 2004; Munoz et al., 2016). For this analysis, the scores of PCs with eigenvalues greater than zero were entered in the form of variables to maintain the whole dimensionality of the tangent space. Centroid size as a covariate for the size-dependent shape modification was entered (Klingenberg, 2010; Klingenberg et al., 2010). The method calculates GP^{-1} (eigenvalues and eigenvectors), where G and P are respectively the genetic and phenotypic covariance matrix. These eigenvalues and eigenvectors provide useful information on the inheritance of shapes, such as the range of heritabilities for all possible shape variables and the shape variables which more or less efficiently react to selection (Klingenberg et al., 2001). With the multivariate generalization of the breeder's equation in quantitative genetics, all the data on the geometric morphometric form are maintained in the study, and the analysis based on the animal model is realistic. The scale and directions of the inheritance of structure are correctly calculated (Klingenberg & Monteiro, 2005). It provides a phenotypical and genotypic covariance in quantitative evolutionary genetics, that is studied through geometric morphometrics. The multivariate generalization algorithm was used for the caste-specific quantitative genetic heritability of females of the caste system of the Asian weaver ant (Lande, 1979). Based on the quantitative genetic response, we can predict the short-term response to selection on various features of shape (Karthika et al., 2021; Anand et al., 2022).



Figure 1. Selected landmarks used for geometric morphometric analysis.

Evolutionary analysis of shape. Mapping shapes onto a phylogenetic tree is an integral part of comparative morphological studies. The modular system Mesquite V3.61 was used for ancestral state reconstruction (Maddison & Maddison, 2016). Two types of phylogenetic analyses (shape and size) were done in this study. To construct and visualize evolutionary shape changes, we mapped the PC scores onto phylogeny, and for size-related phylogeny, the symmetrical body size was computed as the centroid size (CS) (Maddison, 1991; Klingenberg & Gidaszewski, 2010; Žikić et al., 2017). To check the phylogenetic signal of symmetrical body size and shape, we used a permutation method (10000 permutations) to simulate the null hypothesis in the absence of phylogenetic structure by randomly reassigning the shape configuration to the terminal nodes of the phylogeny (Klingenberg & Gidaszewski, 2010; Žikić et al., 2017; Karthika et al., 2021; Anand et al., 2022).

Evolutionary time scale analysis. Evolutionary lineage of the order Hymenoptera, family Formicidae and the subfamily Formicinae were constructed in TimeTree (Kumar et al., 2022). The TimeTree is a public knowledge base on the evolution of life. The time tree of a species group or custom list is constructed in the TimeTree database (Hedges et al., 2015; Kumar et al., 2022; Anand & Shibu Vardhanan, 2020). NWK file format of Hymenoptera order and Formicidae family evolutionary lineage were downloaded from the TimeTree database, and trees were modified by using MEGA X (Kumar et al., 2018). The geographical distribution map of *O. smaragdina* was constructed by using the Antmaps.org server (Janicki et al., 2016).

RESULTS

Quantitative genetic analysis. The 22 eigenvalues were extracted or observed in the major worker ants (Fig. 2, A1; Table 1). It indicated the heritability of particular shape features. The eigenvalue of the matrix GP^{-1} decreased gradually from 55.33 to 1.01. These values show the genetic inheritance of shape changes represented as linear combinations of the landmark coordinates. In the eigenvalue, maximum heritability shape changes correspond to the first eigenvalues, and these shape changes were associated with PC1 of the phenotypic covariations. The low value of the eigenvector indicated minimal heritability.

In major worker ants, the eigenvalues (heritability corresponded to the shape) are 55.33%, followed by 24.84%, and other variables are below 10%. Based on the variance ratio, around 80% of shapes were highly conserved and are inherited from one generation to another generation. The highest eigenvalue shows the shape changes in the thoracic region of major worker ants based on the eigenvalue matrix. The thoracic parts of the major worker ants independently respond to the genetic selection, and it existed as a single module. The abdomen region is dynamically well constrained in Vector 1 (maximum inheritance) (Fig. 2, A2). The minimal heritability analysis (vector 22) of major worker ants showed the tendency to increase the length of the body rather than its width (Fig. 2, A3).

In minor worker ants, the 22 eigenvalues were identified for the respective shape feature analysis; the first eigenvalue covered 53.23% of shape heritability followed by 7.33%, and other eigenvalues were below 3% (Fig. 2, B1; Table 1). Considering the first two set heritability indices, around 60% of shape is conserved. The highest eigenvalue (Vector 1), covered the highest shape changes in the thorax followed by the head and abdomen. By analyzing the heritability statistics, overall analysis supported the enlargement of body size in minor worker ants in a multidimensional projected manner. In the case of head, landmarks 1 & 2 - mandibles are moved into the anterior side (narrowing and lengthening of mandible) and widening the posterior part of the head (landmarks 5 & 6) (Fig. 2, B2). The minimal heritability statistics were analyzed by using the last eigenvector (vector 22); this result supports the lengthening and narrowing (body size decreasing) of minor worker ants. Based on the analysis, we can conclude that the (vector 22) lengthening of the whole body and widening of the head of a minor worker ant is the least selection response (Fig. 2, B3). In selection differential, widening of the head and prothoracic region occur in all possible outward directions. The impact of the prothoracic region

widening is slightly altering the shape of mesothoracic region. The backward movement of the thoracic region (landmarks 7, 8, 9 & 10) leads to the projection of the prothoracic region above the plane of the body (this is one of the major characters present in the queen of *O. smaragdina*), and it will maintain the proper energy distribution dynamics (in carrying weight). The selection gradient and selection differential of a minor worker ant is almost similar. The abdominal region landmarks were focused on the inward direction; it indicated the shape constraint of the abdomen. The total response outcome supported the selection differential outcome of the minor worker ants. The head region shape moves towards all possible directions, the head more or less globular in the posterior side, but in an anterior direction directly forwarded that will help the mandibular process and their dynamic functions (Fig. 2, B4–8). In the *Queen*, by analyzing GP⁻¹, a total of five-set of eigenvalues existed. Out of five eigenvectors, the first four eigenvalues are the same (1.071) and the last one or 5th eigenvalue is 0.642 (Fig. 2, C1; Table 1). This means that, most of the queen shape articulation is highly genetically conserved. In heritable statistics analysis, the highest heritability was expressed in vector 1; based on the functional selection, the prothorax region is inherited more or less globular manner but counteract results were observed in meso and metathorax regions, the starting point of mesothorax a construction occurred and the landmarks move outside towards to the wing articulation regions (landmarks 13 & 14).

Table 1. Heritabilities of the respective shape eigenvalues.

No	Major	Minor	Queen	Worker - media caste	Winged-wingless
1	55.33060	53.23827	1.071429	1	1.004728
2	24.84983	7.330023	1.071429	1	1.004728
3	5.389494	3.683009	1.071429	1	1.004728
4	4.968364	3.400740	1.071429	1	1.004728
5	3.277655	2.879288	0.642857	1	1.004728
6	3.110010	2.350343	-	1	1.004728
7	2.173689	2.270343	-	1	1.004728
8	2.154428	1.984488	-	1	1.004728
9	1.890330	1.875230	-	1	1.004728
10	1.672400	1.770510	-	1	1.004728
11	1.591063	1.615472	-	1	1.004728
12	1.504950	1.479511	-	1	1.004728
13	1.441626	1.440257	-	1	1.004728
14	1.344024	1.349137	-	1	1.004728
15	1.299051	1.222462	-	1	1.004728
16	1.221952	1.128847	-	1	1.004728
17	1.194428	1.118813	-	1	1.004728
18	1.135033	1.088364	-	1	1.004728
19	1.072829	1.056506	-	1	1.004728
20	1.063518	1.024187	-	1	1.004728
21	1.019940	1.011104	-	1	1.004728
22	1.010374	1.008567	-	1	1.004728
23	-	-	-	1	1.004728
24	-	-	-	1	1.004728
25	-	-	-	1	1.004728
26	-	-	-	1	1.004728
27	-	-	-	1	1.004728
28	-	-	-	1	0.134749
29	-	-	-	1	0.033736

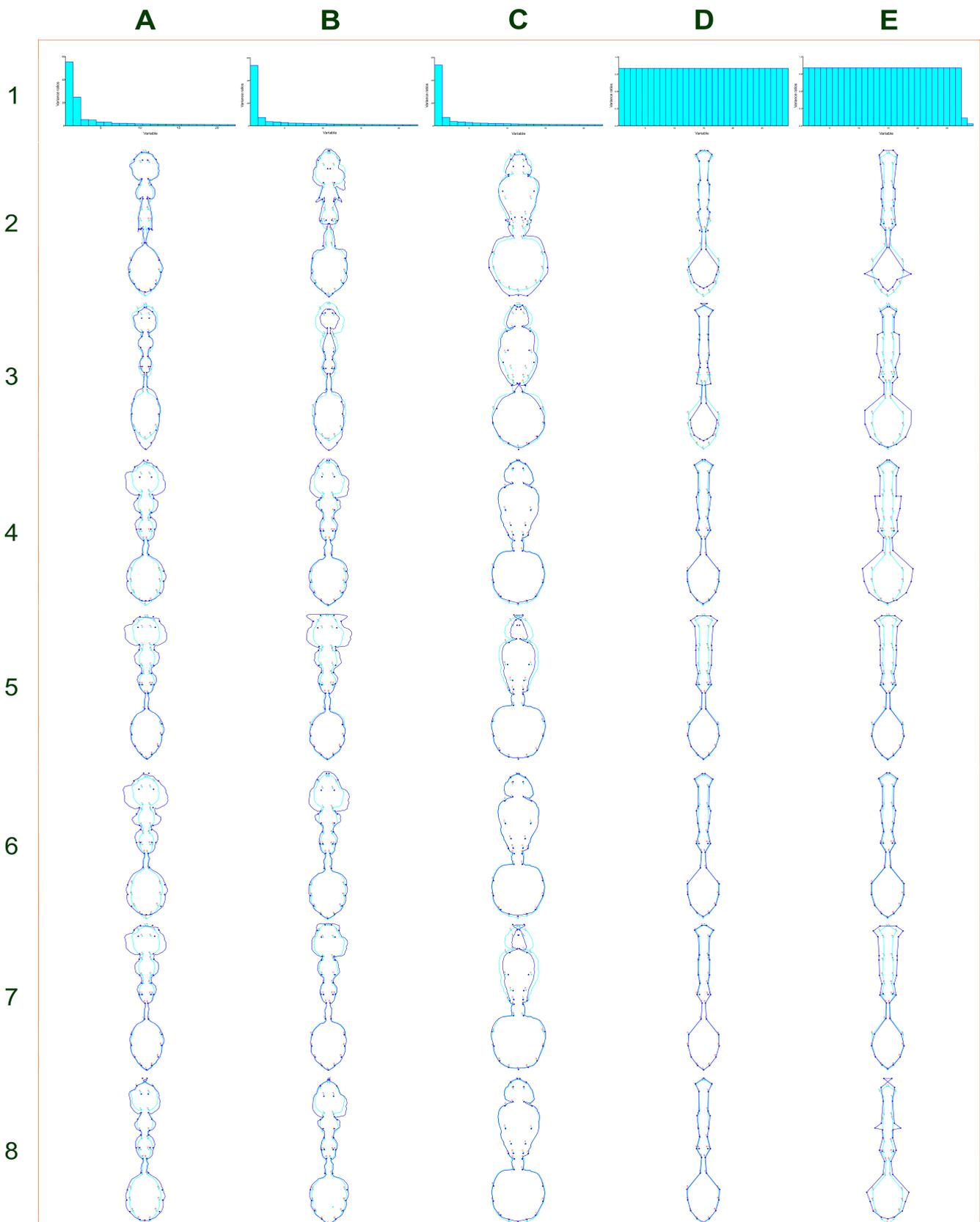


Figure 2. Quantitative genetic analysis and selection responses of female caste of weaver ants. **A.** Major; **B.** Minor; **C.** Queen; **D.** Media caste (worker); **E.** Wingless + Winged form; **1.** Variance ratio; **2.** Vector 1; **3.** Vector 2; **4.** Selection differentials; **5.** Selection gradients; **6.** Total response; **7.** Direct response; **8.** Correlated response.

The queen wing attached into the meso and metathorax, based on these requirements – hence the expansion of these regions was also observed. The queen is the only fertile female individual in the polyphenism caste system of weaver ants, so the major aims are reproduction; based on that the expansion of the abdomen regions is the major characteristic feature which was observed in the maximal heritability vector (Fig. 2, C2). The minimal heritability of linear combination mainly covered the head, abdomen, and prothoracic regions, and it moved into a more constrained structure (to become smaller in size). We can confirm that lengthening of the abdomen is the least selective heritable feature in the queen (Fig. 2, C3). The selection response analysis of queen ants showed some entirely different features compared to the wingless major and minor worker ants. Based on the wing articulations, wing sclerite muscles were highly developed and their developmental imaginal disc maintained degree of slow flight mechanisms. The queen showed highly functionally integrated structures, based on that the selection response is more or less influences the whole symmetrical body. During the selection differential, it validates the before and after parental generation means shape. The head landmarks were moved into the forward direction (anterior), narrowing the head, and it will alter the mandibular process to; small size mandible selection. Only prothoracic regions (Fig. 1, landmarks 9 & 10) showed the widening and other landmarks maintained the body structure in a highly compact manner. Shorting (lengthwise) of the peduncle (Fig. 1, landmarks 19, 20, 21 & 22) is observed in the queen, compared to the worker caste system-queen peduncle is in a very reduced state. The contradictory outcome is observed in the selection gradient, the reduction of head and prothoracic size and highly constructed body system were observed in this selection. Total response selection analysis also supported the previous finding of selection differential. The head regions move in a forwarding direction and narrowing of the mandibular process. The highly complex constraints were observed in meso and metathoracic regions; it may be due to the wing movements and their wing muscle articulations. Overall selection response analysis of queen, the selection differential, total response, and correlated response outcome are almost identical, and similar kinds of responses were also observed in selection gradient and direct response selection responses (Fig. 2, C4–8).

Worker caste (wingless form) revealed a contradictory outcome. In the GP⁻¹ analysis of major-minor combined, the matrix eigenvalue is one and the presence of 29 eigenvalue scores. But in this case, a separate analysis of major and minor worker ants only contained 22 eigenvalue score matrix, with a linear decrease of vector score (Fig. 2, D1; Table 1). Contradictory outcome was observed in the combined effect of major and minor worker ant analysis. In the combined - media caste analysis, the percentage of eigenvalue variations of variables are equally covered without any discriminate modifications. Combined spectrum analysis supported the triphasic allometry of *O. smaragdina*, the different shape and size of major and minor worker ants were connected with intermediate slope-media caste (isometric distribution), and that it can be the reason for the variance ratio becoming one. But by analyzing the highest or maximal heritability of shape were observed in the metathoracic and abdomen regions. The abdomen region landmarks were focused on the inward movement; it indicated as the highly constrained feature of the abdomen and also the presence of well-developed mandible. The minimal heritability of combined major and minor ants covered mainly the abdominal region data mainly, and the maximal (vector 1) (Fig. 2, D2) and minimal (vector 29) (Fig. 2, D3) heritability characters are opposite to each other. *Winged-Wingless system* (queen + worker caste) helps to trace out the average shape of a female caste of weaver ants and their selection responses. Compared to the combined worker caste system (media caste), the same kind of results were also observed in this system (queen and worker caste). Totally 29 eigenvalues and eigenvectors were present in the selection response analysis. The highest heritability matrix score is the same up to the 27th eigenvalues vector matrix (1.004) & the minimal heritability index is 0.033 (29th vector) (Fig. 2, E1; Table 1). Vector 1 of GP⁻¹ matrix analysis, revealed the maximum shape heritability. Compared to only wingless form analysis (major and minor worker caste system), the influence of the winged structure (queen) – alters the gaster structure and was followed by the head, thorax, and mandible (Fig. 2, E2). The minimal heritability mainly influenced on the thoracic region landmarks, expansion of the thorax and abdomen. The reduction of mandibular size and shortening of the peduncle is the least selection characteristic features (Fig. 2, E3).

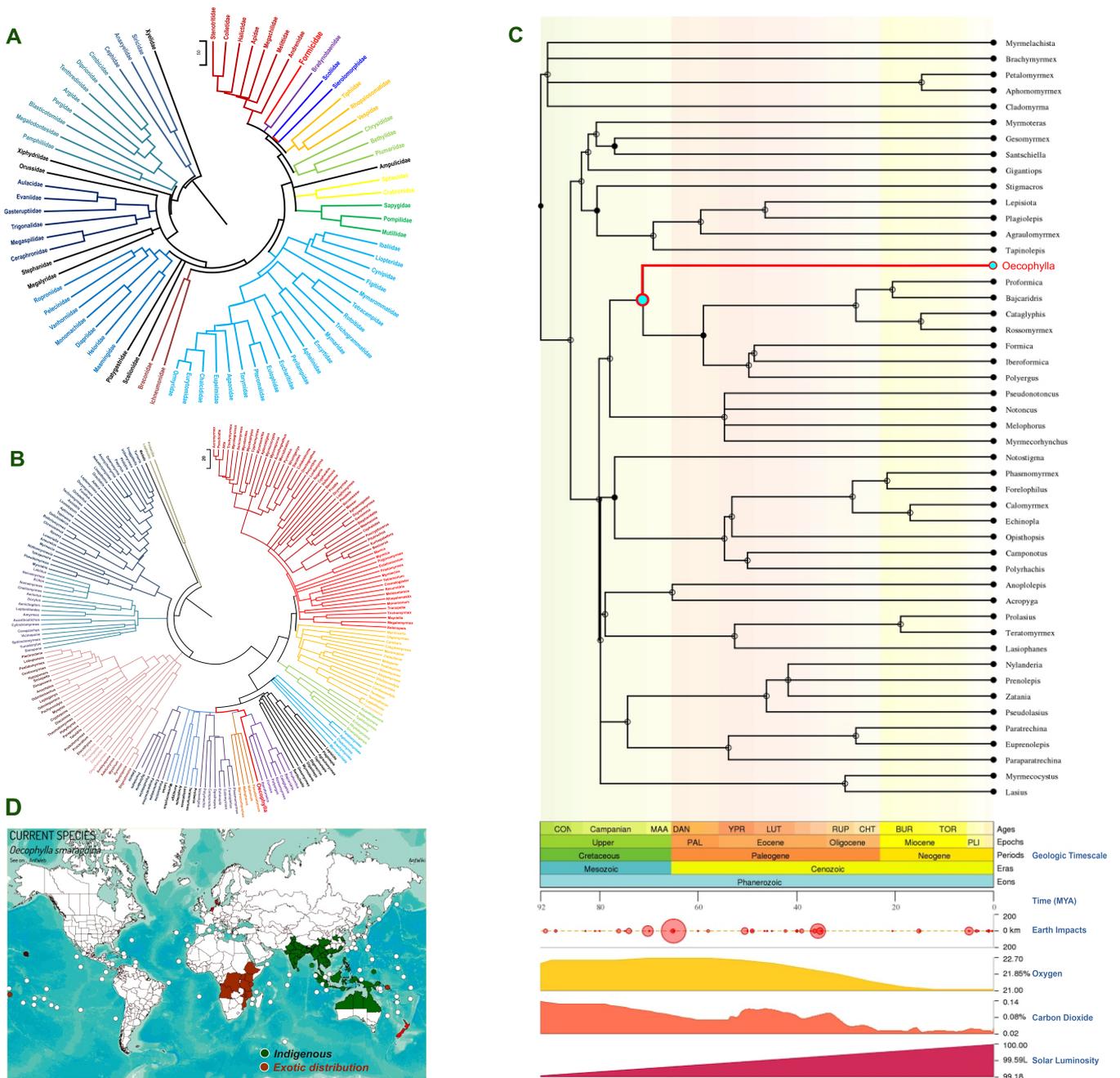


Figure 3. **A.** Evolutionary complexity of Hymenoptera; **B.** Evolutionary complexity of Formicidae; **C.** Evolutionary complexity and lineage of Formicinae (generated in *TimeTree.org* server); **D.** Geographical distribution of *Oecophylla smaragdina* (Asian weaver ant), the color code indicated as green – native distribution & brown – exotic distribution (map generated in *Antmaps.org* server).

Phylogenetic analysis – TimeTree: evolutionary lineage. The highly diverse insect group Hymenoptera appeared at the end of the Paleozoic era (~280 MYA). The evolutionary trace of the formicine subfamily, initially the superfamily Vespoidea group organism, evolved in the middle of the Mesozoic era (~170 MYA). Most of the eusocial organisms evolved during this period and the family Formicidae evolved in ~145 MYA (Fig. 3A). The Formicinae subfamily evolved during ~92 MYA (Fig. 3A). The evolutionary analysis of *Oecophylla* showed unique cladogenesis and speciation process. Totally 23 genera are present in the Formicinae. During the Coniacian age (starting point of the Cretaceous period and upper epochs), the Formicinae evolved. The first cladogenesis was observed during the

~91 MYA, but the ancestor is unknown (the ancestor of most of the genera is unknown). Plagiolepidini (~81 MYA) is the first originated tribe in the evolutionary time scale of Formicinae and followed by Camponotini (~77 MYA) and Gesomyrmecini (~77 MYA), only these tribes evolved during the Cretaceous periods. Genus *Oecophylla* cladogenesis is observed in the Cretaceous period, 71 MYA, but the ancestor is unknown. The descendent of Formicinae, the *Oecophylla* genus, was initially separated, and another cladogenesis was observed in 59 MYA (Formicini tribe). This separation was observed in the Paleocene epoch and the middle of the Selandian age. The genus *Oecophylla* is the second last Formicinae group separated during the Campanian period (83.50–70.60 MYA), the upper epoch. The previously separated group in the upper epoch is the descendant of the Plagiolepidini (69 MYA - Cretaceous period) Maastrichtian age (70.60–65.50 MYA). The descendant of Formicinae is closely related to the tribe Formicini, and the descendant of Formicinae (*Oecophylla* speciation) doesn't show any clad separation or speciation event (during ~72–14 MYA). The low evolutionary variation indicated their preservation of favoured adaptation features (Figs 3B & 3C).

Phylogenetic signal analysis. Five different set groups were used for evolutionary analysis of shape and size (Fig. 4A & 4B). The distribution of the major, minor, queen, wingless system (media caste system) and winged-wingless system in the symmetrical body shape in a morphospace is proved that each organism has a distinct evolutionary origin. The first two PC axes described 99.99% of the total variance in morphological polyphenism (PC1=97.41%, PC2=2.58%). These two PCs clearly separate the female caste system and also the combined structural system in the morphospace. The PC1s is the reduce the dimensionality (without losing variable features) in one space and they mainly covered the head and mesothorax architectural intricate details, and the shape changes of PC1s is included lengthening of the body, narrowing of the abdomen and prothorax regions (major, major + minor and Major + minor + queen).

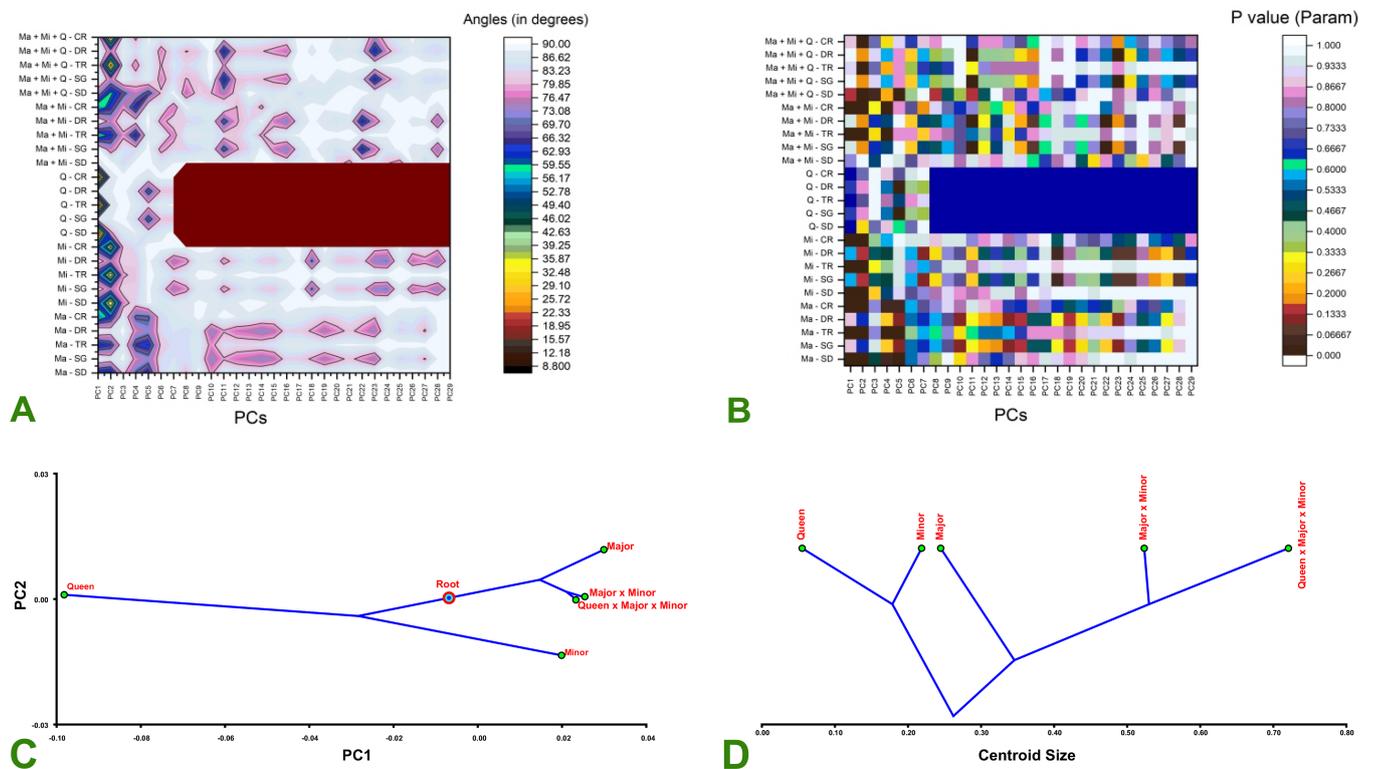


Figure 4. **A.** Vector comparison angle analysis. **B.** P-value of vector angles from tangent space; **C.** Evolution of shape related to PC1 and PC2; **D.** Evolutionary size analysis, centroid size. (SD. Selection differential; SG. Selection gradient; TR. Total response; DR. Direct response; CR. Correlated response; Ma. Major worker ant; Mi. Minor worker ant; Q. Queen).

In the case of PC2, reducing head region size and increasing the size of the prothorax and abdomen (queen and minor) are the major shape changes. We can confirm that the first two PCs (PC1 & PC2) cover all morphological variations of all five different group systems within a specified morphospace. PCs-based phylogeny covered the phenotypic shape similarity and dissimilarity of the caste system and expressed in morphometric space and there is no detectable phylogenetic signal in different caste systems (tree length 0.00086 & $p = 0.293$). The media caste (major + minor) and winged (queen) + wingless (major + minor) system, diverged from the same hypothetical internal node and this node descended from the hypothetical ancestor node of a major worker ant (Fig. 4C). The distribution of morphological landmarks types relative to each caste system size indicates that queen type occurred in a small log-centroid value compared to other groups. It was interesting that the queen and minor worker ants diverged from the same hypothetical ancestor system (this kind of phenomenon was also observed in PC based analysis). Initially, the root is separated into two main clades, one clade for queen and minor workers ant and other clades for other caste systems (major, major + minor and major + minor + queen). No phylogenetic signal was observed in morphological distribution of landmarks with their centroid body size (tree length 0.1113 & $p = 0.096$) in 10000 permutation (Fig. 4D).

DISCUSSION

Oecophylla smaragdina exists as triphasic allometry, i.e., the allometric line separates at two points and consists of three straight lines. The final sections that representing both the small and large castes, are slightly different isometrically while a very steep slope lies in the middle segment, which includes the media caste (Wilson, 1953). Within the minor and major castes, the purposes of three-phase allometry are to stabilize the body proportions. The existence of triphasic allometry, we initially analyzed the evolutionary lineage of our model organisms. Insects are highly evolved, and it shows a wide range of adaptability. The TimeTree analysis helps to understand the origin and nature of life forms in the evolutionary process. It divulges the clock like an overview of transition, speciation, diversity, and events that occurred during the geological time period (Hedges et al., 2015; Anand & Shibu Vardhanan, 2020; Kumar et al., 2022). The *O. smaragdina* comes under the Hymenoptera order and the Formicidae family. The phylogenetic origin lineage analysis from order to genus level helps to characterize their evolvability. Surprisingly we observed that our model organism showed less evolutionary modification and doesn't show too many cladogenesis and speciation events. It means that the natural selection system well supports the morphological architecture complexity of *O. smaragdina* with morphological persistence stability.

Currently, 15 fossil species related to *Oecophylla* have been found from the Eocene (55.80–33.90 MYA) to Miocene (23.03–5.33 MYA) (Azuma et al., 2002; Dlussky et al., 2008). The cladogenesis of the *Oecophylla* genus was observed in the Serravallian age (13.82–11.61 MYA). According to Blaimer et al. (2015), ~70–65 MYA, the *Oecophylla* clad was separated into two clads, *Oecophylla* sp. and *Gesomyrmex* sp. Nevertheless, the *Oecophylla* genus clad was separated during 13.2 MYA, and one clade is formed for *O. smaragdina*, and another for *O. longinoda*. Based on the evolutionary lineage, the weaver ant genus (*Oecophylla*) is relatively old. Currently, the weaver ant genus is provisionally placed in the tribe *Oecophyllini*. The genus contains only two closely related species and distributes in a specified area. The geographical distribution analysis, the origin, and the highest abundance of *O. smaragdina* were observed in tropical and subtropical regions/temperate zone (Azuma et al., 2002; Wettere, 2017). The ancestral organisms evolved or formed in the Oriental regions and Australian regions and have distributed in Neotropical, Ethiopian, and some island regions of Australian zoogeographical realms. The low level of evolutionary selection pressure and the morphological, and structural complexity may not be suite for all existing zoogeographical domains (Fig. 3C). Already we said that our model organism is relatively old and shows slow diversifications. The reason for slow diversification may be the high level of functional modular integration and their morphological architecture complexity of

polyphenism (Wheeler, 1991). Genetic variation is the most significant factor in the symmetrical variability of body shape, and the variance of all space measures/dimensions is greater than one when the GP^{-1} matrix is analyzed. Eigenvalues of the matrix GP^{-1} are different from those of the PCs and show that the possibilities for evolutionary changes in response to selection predominantly depend on the attributes. These eigenvalues and eigenvectors provide valuable information on the inheritance of the structures, such as the range of heritability for all possible variables and the form of variables that respond to selection more or less easily (Klingenberg & Leamy, 2001a, 2001b).

The selection differential (according to breeder's equation $\Delta\mu = GP^{-1}s = G\beta$, where $\Delta\mu$ is the response to selection, 'G' is the additive genetic covariance matrix, 'P' is the phenotypic covariance matrix, 's' is the selection differential and ' β ' is the selection gradient (Lande, 1979), the selection differential 's' is the difference between the shape means before and after selection in a parent generation (under truncation selection, or the vector of covariance function between the shape variables and relative fitness) of major worker ants, highly influenced on the frontal part of the head, prothorax and first and last abdominal segments. Widening of the prothoracic and head regions are the major shape changes observed in the selection differential analysis. But in the selection gradient (according to the Breeder's equation, selection differential β evaluate the vector of regression coefficients from a regression of relative fitness of shape) specifically 'hold constant', It indicates the impact of those shape features (morphological shape and size variations of worker and queen of Asian weaver ant) that are phenotypically correlated but not under selection gradient. So, the selection gradient usually favoured for studying directional selection (Lande, 1979; Lande & Arnold, 1983). By analyzing the outcome of the selection differential, the major workers have tendencies to increase the width of the whole body in a dynamic proportional manner to maintain the body structure. In selection response analysis, the highly influenced body parts are the head (the major sensilla regions such as antennae and eye and mouthparts) followed by thorax. It is not possible to make a very useful generalization about the widening of head. The widening of the head may be also affected the shape and size of mandibles – the basic pattern of the mandible may get evolutionarily modified and adapted to exploit a different kind of functions (outdoor tasks and defense mechanisms) (Fig. 2, A4–8).

Analyzing the heritability statistics, selection differential analysis - the matrices GP^{-1} influences the shape of the thoracic region. The expansion of the head region was the major characteristic feature observed in major workers. But in the selection gradient, the highly influenced part is the head and followed by the thoracic region – this result is similar to the minor worker ants. In total response, the most influenced part is the prothoracic regions. Head followed by thorax and abdomen are the highly influenced parts in direct response analysis, and also the most constrained shape is observed in correlated response. The progressive decreasing shape response is a critical factor for functional-based energy management and its distribution. The combined system of worker ants, the media caste, expressed the mixed characteristic features of major and minor workers (Fig. 2, D4–8). In the selection response analysis of the winged-wingless form, each selection response showed unique characteristic shape movements and articulations. Initially, we postulated that the worker and queen descended from a single common ancestor, and that this ancestor may have exhibited a combination of the morphological traits shared by both the worker and the queen. As evidence for our findings, the majority of shape and size variations were found in the thoracic and head regions in the combined form ant (i.e., winged-wingless form). The shape features include a large, globular gaster (a queenly trait), a large head, and a long, slender mandibular process (a combination of major and worker ant phenotypic characters) (Fig. 2, E4–8). The correlated response is not only a significant part of the overall selection effect but also provides important data on the geometry of the selection process/response (Klingenberg & Leamy, 2001a, 2001b). The evolutionary potential of the ant caste system's morphological structure may be taken into consideration. Based on the heritability statistics, we confirmed that functional modular integration exists in queen, major, and minor worker ants (female caste system – morphological polyphenism) (Table 2).

Table 2. Predicted response to directional selection (Selection response) of major, minor, queen, major + minor (media) system and major + minor + queen system.

Sl. No	Analysis	Major	Minor	Queen	Major + Minor	Major + Minor + Queen
1	Selection differential					
	Magnitude in unit of Procrustes distance	1.5665	4.860	0.463	0.357	1.160
	Magnitude in unit of phenotypic standard deviation	154.699	417.949	21.583	36.351	62.067
2	Selection gradient					
	Magnitude – Standardized by phenotypic variation in the same direction	277.342	458.974	25.932	44.440	70.373
3	Total response to selection					
	Magnitude in unit of Procrustes distance	1.717	5.210	0.461	0.357	0.288
4	Direct response selection (based on the direction of the selection gradient)					
	Magnitude in unit of Procrustes distances	0.959	2.151	0.066	0.175	0.145
5	Correlated response to selection					
	Magnitude in unit of Procrustes distances	1.423	4.745	0.457	0.311	0.249

The widening and lengthening of the head region also alter the mandibular process – it may help the major worker ants for defense and foraging purposes and other nest-building function aspects. The primary function of a minor worker ant is brood care, so that purposes the mandibular process is not much expanded; it moves to the reduced state condition (Babu et al., 2011).

Finally, we can conclude that the ecological specification in many taxa is correlated with the head and its muscle structures, mostly, but not limited to, feeding functions. Therefore, head structural divergence in major and minor workers likely due to differences in colony tasks (Smith 1987; Mertl & Traniello, 2009). Castes are a more dynamic product of adaptive evolution (Powell et al., 2020). From this perspective, weaver ant showed different selection responses. The quantitative genetic study of shape selection response would provide new insights into the genetic base of adaptive alteration and the underlying nature of morphological structures. Highly altered and conserved regions in symmetrical body structures and their heritability level study will help to explore the speciation and diversification of morphological polyphenism. Genetic level alterations and their related morphological variations as well as shape and size heritability can be easily studied by using a multivariate quantitative genetic analysis (Klingenberg et al., 2001; Klingenberg & Leamy, 2001a, 2001b).

There is no detectable shape and size phylogenetic signal in the females of *O. smaragdina*. These findings supported the divergent evolution of the symmetrical body shape of the caste system, and the architectural morphological complexity of each system (caste) was separately derived (and also the presence of some degree of homoplasy). This kind of phenomenon was observed in *Drosophila melanogaster* subgroup - sexual shape dimorphism, lack of a detectable phylogenetic signal may result from a selection of a phylogenetic structure that is dominated or instead, maybe the result of spontaneous random drift evolution (combination with speciation and founder effects) (Gidaszewski et al., 2009). A strong phylogenetic signal means that closely related species are more similar in shape than in structure (morphological architecture) in distally related species. In other words, closely related species should share the same morphometric space, whereas more remote species should be located in different and potentially remote locations. In contrast, data lacking a phylogenetic signal have a tendency to result in more pronounced shape changes on the phylogenetic branches because closely related species are predicted to be equally distant from one another as remotely related species. A strong phylogenetic signal is expected to result in a significantly smaller amount of change on the

entire tree than it would in the absence of one (Klingenberg & Gidaszewski, 2010). The evolutionary heterogeneity makes ant phylogeny very complex and challenging to recognize or to decode the tree root features. The overall morphology (advanced morphometric tool-based) analysis helps to better understand the relationship between fossils and current taxa and makes them more effective in dating divergence, but also provides a pragmatic structure to classify living organisms. Better morphological characterization of species and higher taxa helps to investigate consistency in habitats and shapes (Ward, 2014). Ant body size can evolve faster than body shape. Many species (Stanley & Yang, 1987; Clyde & Gingerich, 1994; Hunt, 2007; Wood et al., 2007; Dzeverin, 2008) have been found with similar size and shape variations and they are often interpreted as a sign that size will tend to be more evolutionarily labile (Stanley, 1979). Organisms can undergo an evolutionary transition by altering the axis of their size, which entails altering their allometry, such as whether it is positively or negatively allometric or, isometric axis (Marroig & Cheverud, 2005 & 2010). This strategy might operate in colonies so that the morphological variability can be accomplished by adjusting the size of the body (allometry) rather than modifying the shape (Pie & Tscha, 2013). Unusual triphasic allometry is exhibited by Asian weaver ants (Wilson, 1953), so changes in allometry affect their morphological structure and may make it easier for them to carry out colony tasks (Mahima et al., 2021).

This is the first study report explaining the shape heritability of the female caste system in the Asian weaver ant. The shape and size inheritance of the queen and workers (major and minor) castes were revealed in this study. We tracked each caste's morphological functional divergence using quantitative genetic analysis. The widened head, well-developed mouthparts, and thoracic regions are highly heritable traits of major worker ants that indicate function adaptation of the major workers and these morphological characters help to perform outdoor tasks (i.e., foraging and defense). Long and slender body features are highly heritable traits in minor worker ants that are modulated for indoor tasks, especially for maintaining the brood. It's interesting to note that the major heritable traits in queens are well-developed thorax and abdomen, which indicate the ability to fly and to produce offspring, respectively. According to the results of the phylogenetic signal analysis, all shape and size characteristics of each caste are influenced by environmental factors rather than by evolutionary factors. In the phylogeny analysis, we also revealed that, minor workers showed a closer relationship with queen than major worker. It indicated the morphological divergence and evolution of eusocial organization in Asian weaver ants. Our research indicates that Asian weaver ants have a high degree of environmental adaptability because environmental factors control the changes in their size and shape. This peculiar characteristic was the main factor in the Asian weaver ants' global distribution. We deduced from the study that Asian weaver ants had caste-specific shape and size variations, and these variations were influenced/modulated by their functional activities.

AUTHOR'S CONTRIBUTION

The authors confirm their contribution to the paper as follows: Conceptualization: P.P.A. Conceiving and designing the experiment: P.P.A. & Y.S.V. Digitalization and landmarking of specimens: K.V.M. & P.P.A. Software: P.P.A. & Y.S.V. Analysis and interpretation of the data: P.P.A, K.V.M. & Y.S.V. Writing the main manuscript: PPA. Drawing & photographic plate preparation: Y.S.V. Supervision: Y.S.V. All authors reviewed the results and approved the final version of the manuscript.

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AVAILABILITY OF DATA AND MATERIAL

Not applicable.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

Not applicable.

CONSENT FOR PUBLICATION

Not applicable.

CONFLICT OF INTERESTS

The authors declare that there is no conflict of interest regarding the publication of this paper.

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Appendix 1 (Table S3) Angular comparison of vector direction, Angle in degrees, **SD**. Selection differential; **SG**. Selection gradient; **TR**. Total response; **DR**. Direct response; **CR**. Correlated response

	MAJOR						MINOR						QUEEN					
	SD	SG	TR	DR	CR	SD	SG	TR	DR	CR	SD	SG	TR	DR	CR			
PC1	59.958	88.495	59.155	88.495	53.085	63.488	84.009	62.29	84.009	62.404	14.064	85.641	8.832	85.641	9.066			
PC2	57.48	85.181	64.5	85.181	62.447	32.078	74.479	33.078	74.479	36.993	78.483	88.052	86.278	88.052	86.523			
PC3	81.867	89.272	86.926	89.272	86.783	77.053	82.562	79.101	82.562	81.436	86.356	89.749	89.678	89.749	89.711			
PC4	69.102	77.606	64.77	77.606	68.324	82.856	81.868	81.2	81.868	84.04	88.431	83.238	87.395	83.238	88.352			
PC5	63.056	72.821	62.107	72.821	68.587	88.918	89.106	89.471	89.106	89.825	84.308	65.219	82.834	65.219	86.276			
PC6	83.68	83.448	81.367	83.448	84.024	86.174	83.813	86.981	83.813	89.487	86.366	80.637	87.899	80.637	89.236			
PC7	86.848	85.113	83.837	85.113	85.868	87.112	73.48	84.023	73.48	89.163	89.951	79.915	88.914	79.915	89.635			
PC8	79.587	84.062	84.348	84.062	87.189	87.478	77.965	86.466	77.965	88.461	-	-	-	-	-			
PC9	89.985	86.09	86.93	86.09	88.933	88.756	86.776	89.201	86.776	89.417	-	-	-	-	-			
PC10	78.596	72.475	77.992	72.475	87.254	88.132	86.199	89.12	86.199	89.244	-	-	-	-	-			
PC11	88.055	79.331	84.52	79.331	89.449	87.358	77.484	87.568	77.484	87.037	-	-	-	-	-			
PC12	86.289	76.095	83.722	76.095	88.275	88.126	82.612	88.699	82.612	88.087	-	-	-	-	-			
PC13	85.157	75.005	83.569	75.005	87.746	89.429	85.618	89.321	85.618	88.761	-	-	-	-	-			
PC14	86.504	72.585	84.036	72.585	85.616	89.385	82.098	88.881	82.098	87.656	-	-	-	-	-			
PC15	88.52	74.761	85.512	74.761	85.25	87.26	81.183	88.98	81.183	87.136	-	-	-	-	-			
PC16	88.139	82.636	87.866	82.636	87.622	89.726	85.789	89.577	85.789	88.557	-	-	-	-	-			
PC17	89.396	82.197	88.123	82.197	87.018	88.904	89.213	89.928	89.213	89.722	-	-	-	-	-			
PC18	88.919	79.052	88.049	79.052	85.011	89.643	68.586	88.307	68.586	82.35	-	-	-	-	-			
PC19	87.941	73.869	87.338	73.869	82.458	89.835	87.47	89.821	87.47	89.049	-	-	-	-	-			
PC20	88.254	77.968	88.601	77.968	83.624	89.85	81.387	89.55	81.387	86.601	-	-	-	-	-			
PC21	89.318	81.18	89.008	81.18	85.268	89.495	80.635	89.55	80.635	86.264	-	-	-	-	-			
PC22	89.946	77.535	88.76	77.535	83.143	89.847	82.625	89.674	82.625	87.021	-	-	-	-	-			
PC23	89.645	72.931	88.639	72.931	80.258	89.941	72.168	89.356	72.168	82.731	-	-	-	-	-			
PC24	89.481	86.985	89.797	86.985	88.213	89.795	70.753	89.357	70.753	82.116	-	-	-	-	-			
PC25	89.729	82.621	89.563	82.621	85.562	89.829	87.429	89.935	87.429	88.906	-	-	-	-	-			
PC26	89.875	83.603	89.64	83.603	86.129	89.558	75.264	89.675	75.264	83.736	-	-	-	-	-			
PC27	89.967	79.285	89.469	79.285	83.446	89.929	77.867	89.759	77.867	84.797	-	-	-	-	-			
PC28	89.896	88.44	89.927	88.44	89.037	89.942	71.739	89.745	71.739	82.114	-	-	-	-	-			
PC29	89.874	89.652	89.997	89.652	89.769	89.97	85.019	89.986	85.019	87.758	-	-	-	-	-			

Appendix 2 (Table S4). Angular comparison of vector direction, Angle in degrees, **SD**. Selection differential; **SG**. Selection gradient; **TR**. Total response; **DR**. Direct response; **CR**. Correlated response

	WORKER CASTE					MINOR				
	SD	SG	TR	DR	CR	SD	SG	TR	DR	CR
PC1	87.173	89.344	53.856	89.344	53.495	73.844	89.869	88.704	89.869	88.576
PC2	89.998	75.969	62.012	75.969	64.041	58.156	75.268	23.759	75.268	24.283
PC3	83.154	85.24	78.242	85.24	78.845	67.78	88.652	86.378	88.652	86.593
PC4	89.611	83.118	60.708	83.118	61.534	76.353	83.797	76.997	83.797	78.611
PC5	89.391	89.632	87.996	89.632	87.917	66.194	87.994	88.008	87.994	88.866
PC6	85.902	77.729	87.778	77.729	85.891	80.757	77.159	79.533	77.159	85.383
PC7	88.343	82.72	77.348	82.72	76.06	89.599	84.05	85.777	84.05	88.586
PC8	88.737	82.593	87.773	82.593	88.875	74.885	79.591	83.16	79.591	88.148
PC9	89.488	83.876	87.656	83.876	86.695	82.395	81.171	85.542	81.171	89.983
PC10	87.613	86.215	85.893	86.215	85.266	79.905	89.776	89.898	89.776	89.987
PC11	89.239	65.587	83.532	65.587	87.084	74.237	59.791	79.287	59.791	85.476
PC12	88.525	79.191	81.368	79.191	79.605	82.169	81.018	87.147	81.018	88.073
PC13	87.706	83.137	85.738	83.137	84.64	89.751	81.285	87.443	81.285	87.884
PC14	89.514	89.435	78.657	89.435	78.436	87.253	80.189	87.497	80.189	87.189
PC15	89.032	76.506	85.763	76.506	87.758	85.62	78.061	87.36	78.061	86.124
PC16	84.742	71.001	87.881	71.001	85.004	88.134	75.501	87.249	75.501	84.791
PC17	85.344	84.445	88.743	84.445	87.882	83.844	89.975	89.996	89.975	89.99
PC18	87.558	89.149	89.404	89.149	89.267	86.113	87.41	89.573	87.41	88.98
PC19	88.885	86.805	89.163	86.805	88.666	84.874	89.753	89.965	89.753	89.896
PC20	82.088	84.453	89.189	84.453	89.975	88.429	84.978	89.405	84.978	87.756
PC21	78.065	86.816	89.529	86.816	89.991	89.947	87.159	89.748	87.159	88.631
PC22	87.813	60.119	87.683	60.119	83.286	89.692	83.532	89.482	83.532	86.825
PC23	85.341	75.927	89.783	75.927	87.654	87.461	59.479	87.836	59.479	75.333
PC24	80.275	85.949	88.642	85.949	89.244	88.403	78.159	89.213	78.159	84.026
PC25	77.132	89.562	89.633	89.562	89.562	85.416	83.674	89.635	83.674	86.729
PC26	88.363	87.609	89.346	87.609	89.703	88.056	87.667	89.879	87.667	88.776
PC27	82.222	88.247	88.452	88.247	88.702	86.514	84.066	89.732	84.066	86.846
PC28	86.334	71.072	89.699	71.072	87.467	89.52	82.859	89.719	82.859	86.158
PC29	89.871	89.918	89.381	89.918	89.361	89.589	85.676	89.954	85.676	87.526

Appendix 3 (Table S5). Angles in vector direction *p*-value (parametric). **SD**. Selection differential; **SG**. Selection gradient; **TR**. Total response; **DR**. Direct response; **CR**. Correlated response

	MAJOR						MINOR						QUEEN					
	SD	SG	TR	DR	CR	SD	SG	TR	DR	CR	SD	SG	TR	DR	CR			
PC1	0.00484	0.89042	0.00377	0.89042	0.00045	0.01341	0.58306	0.00962	0.58306	0.00994	<.00001	0.68977	<.00001	0.68977	<.00001			
PC2	0.00219	0.65898	0.01756	0.65898	0.01006	<.00001	0.15283	<.00001	0.15283	<.00001	0.29015	0.85844	0.73326	0.85844	0.75024			
PC3	0.45587	0.94687	0.77835	0.94687	0.76837	0.23396	0.49537	0.31699	0.49537	0.43226	0.73862	0.98164	0.97645	0.98164	0.97888			
PC4	0.05299	0.2547	0.01884	0.2547	0.04456	0.51264	0.45591	0.41961	0.45591	0.58504	0.88583	0.53549	0.81153	0.53549	0.88009			
PC5	0.01192	0.11307	0.00914	0.11307	0.04728	0.92111	0.93475	0.96141	0.93475	0.98723	0.60203	0.02113	0.51133	0.02113	0.73309			
PC6	0.56255	0.54827	0.42851	0.54827	0.58402	0.72612	0.57079	0.78225	0.57079	0.96255	0.73935	0.39034	0.84745	0.39034	0.94422			
PC7	0.77287	0.65446	0.57228	0.65446	0.70516	0.79144	0.12778	0.58396	0.12778	0.93893	0.99642	0.35467	0.92083	0.35467	0.97332			
PC8	0.33918	0.5864	0.60459	0.5864	0.79691	0.81743	0.26884	0.74622	0.26884	0.88795	-	-	-	-	-			
PC9	0.99887	0.72028	0.77863	0.72028	0.92218	0.90936	0.76787	0.94167	0.76787	0.95741	-	-	-	-	-			
PC10	0.29493	0.10587	0.26994	0.10587	0.80149	0.86424	0.72783	0.93582	0.72783	0.94481	-	-	-	-	-			
PC11	0.85866	0.32736	0.61564	0.32736	0.95978	0.8089	0.25002	0.82384	0.25002	0.78619	-	-	-	-	-			
PC12	0.73399	0.20083	0.56511	0.20083	0.87451	0.8638	0.49829	0.90521	0.49829	0.86099	-	-	-	-	-			
PC13	0.65734	0.16742	0.55568	0.16742	0.83653	0.95834	0.68822	0.95042	0.68822	0.90968	-	-	-	-	-			
PC14	0.74892	0.10812	0.58478	0.10812	0.6881	0.95512	0.46877	0.9184	0.46877	0.8301	-	-	-	-	-			
PC15	0.89222	0.16053	0.68105	0.16053	0.66356	0.80194	0.41873	0.92565	0.41873	0.79315	-	-	-	-	-			
PC16	0.86473	0.49966	0.8451	0.49966	0.82767	0.97996	0.6998	0.96911	0.6998	0.89489	-	-	-	-	-			
PC17	0.95594	0.47441	0.86361	0.47441	0.78484	0.92006	0.94259	0.99476	0.94259	0.9797	-	-	-	-	-			
PC18	0.92121	0.31478	0.85823	0.31478	0.64772	0.97396	0.04728	0.87684	0.04728	0.48313	-	-	-	-	-			
PC19	0.85052	0.13714	0.80743	0.13714	0.48932	0.98798	0.81681	0.98694	0.81681	0.93065	-	-	-	-	-			
PC20	0.87302	0.26897	0.89807	0.26897	0.55904	0.98907	0.42957	0.96715	0.42957	0.75563	-	-	-	-	-			
PC21	0.95023	0.41853	0.92767	0.41853	0.66476	0.96313	0.39024	0.96712	0.39024	0.73226	-	-	-	-	-			
PC22	0.99608	0.25197	0.90962	0.25197	0.52973	0.98882	0.49905	0.97621	0.49905	0.78508	-	-	-	-	-			
PC23	0.97406	0.11542	0.90086	0.11542	0.37136	0.9957	0.0998	0.95299	0.0998	0.50527	-	-	-	-	-			
PC24	0.96209	0.78252	0.9852	0.78252	0.87003	0.98503	0.07526	0.95308	0.07526	0.46982	-	-	-	-	-			
PC25	0.98023	0.49879	0.96808	0.49879	0.68445	0.98748	0.81391	0.99523	0.81391	0.92024	-	-	-	-	-			
PC26	0.99086	0.5578	0.97368	0.5578	0.72298	0.96771	0.17497	0.97628	0.17497	0.56598	-	-	-	-	-			
PC27	0.99759	0.32525	0.96121	0.32525	0.5481	0.99481	0.26493	0.9824	0.26493	0.63363	-	-	-	-	-			
PC28	0.99244	0.88643	0.99464	0.88643	0.92974	0.99579	0.09178	0.9814	0.09178	0.46966	-	-	-	-	-			
PC29	0.99077	0.97457	0.9998	0.97457	0.9831	0.99781	0.64823	0.99901	0.64823	0.83741	-	-	-	-	-			

Appendix 4 (Table S6). Angles in vector direction p -value (parametric). **SD**. Selection differential; **SG**. Selection gradient; **TR**. Total response; **DR**. Direct response; **CR**. Correlated response

	MAJOR					MINOR				
	SD	SG	TR	DR	CR	SD	SG	TR	DR	CR
PC1	0.79576	0.95212	0.0006	0.95212	0.00053	0.13651	0.99042	0.90558	0.99042	0.89626
PC2	0.99987	0.19673	0.00889	0.19673	0.01556	0.00273	0.17507	<.00001	0.17507	<.00001
PC3	0.53041	0.66289	0.28011	0.66289	0.30566	0.03935	0.9018	0.74014	0.9018	0.75507
PC4	0.97163	0.52822	0.00607	0.52822	0.00775	0.20942	0.56977	0.23191	0.56977	0.29559
PC5	0.95552	0.97315	0.85448	0.97315	0.84878	0.02697	0.8543	0.85532	0.8543	0.91731
PC6	0.70744	0.2595	0.83882	0.2595	0.70673	0.39647	0.23783	0.33665	0.23783	0.67239
PC7	0.87944	0.5046	0.24487	0.5046	0.1997	0.9707	0.58566	0.69898	0.58566	0.89699
PC8	0.90794	0.49715	0.83849	0.49715	0.91801	0.16401	0.33935	0.53078	0.33935	0.86539
PC9	0.96262	0.57472	0.83008	0.57472	0.76217	0.48573	0.41809	0.68308	0.41809	0.99875
PC10	0.82704	0.7289	0.70685	0.7289	0.66463	0.35421	0.98361	0.99255	0.98361	0.99904
PC11	0.94446	0.02319	0.55341	0.02319	0.78946	0.14646	0.00459	0.32538	0.00459	0.67867
PC12	0.89259	0.32104	0.4286	0.32104	0.34001	0.47278	0.41002	0.79392	0.41002	0.85999
PC13	0.83368	0.52937	0.69634	0.52937	0.62347	0.98185	0.42411	0.81491	0.42411	0.84643
PC14	0.96451	0.95873	0.29755	0.95873	0.28817	0.80143	0.36799	0.81875	0.36799	0.79692
PC15	0.92937	0.21461	0.69804	0.21461	0.83737	0.68834	0.27271	0.80898	0.27271	0.72268
PC16	0.6301	0.07918	0.8462	0.07918	0.64728	0.86435	0.18208	0.80114	0.18208	0.63328
PC17	0.66982	0.61082	0.90841	0.61082	0.84625	0.57274	0.99815	0.99969	0.99815	0.99928
PC18	0.82309	0.9379	0.9565	0.9379	0.94653	0.7219	0.81258	0.96885	0.81258	0.92564
PC19	0.91871	0.76991	0.93894	0.76991	0.90282	0.63869	0.98196	0.99748	0.98196	0.99237
PC20	0.46824	0.61134	0.94085	0.61134	0.99816	0.88563	0.64553	0.95658	0.64553	0.83723
PC21	0.27286	0.77063	0.96561	0.77063	0.99933	0.99612	0.79482	0.98163	0.79482	0.90028
PC22	0.84134	0.00508	0.83202	0.00508	0.53836	0.97748	0.55341	0.96216	0.55341	0.77129
PC23	0.66963	0.19541	0.98413	0.19541	0.82992	0.81618	0.00417	0.84295	0.00417	0.17702
PC24	0.37224	0.71068	0.90105	0.71068	0.94481	0.88375	0.27671	0.94259	0.27671	0.58419
PC25	0.23685	0.968	0.97319	0.968	0.968	0.6746	0.56219	0.97338	0.56219	0.7646
PC26	0.88086	0.82677	0.95228	0.82677	0.97834	0.85874	0.83086	0.99117	0.83086	0.9108
PC27	0.47583	0.8725	0.88734	0.8725	0.90542	0.74958	0.58665	0.9804	0.58665	0.77274
PC28	0.73714	0.08031	0.97804	0.08031	0.81665	0.96496	0.51281	0.97949	0.51281	0.72499
PC29	0.99055	0.994	0.9548	0.994	0.95337	0.96997	0.69215	0.99667	0.69215	0.82085

آشکارسازی ریخت‌سازگاری مورچه بافنده آسیایی، *Oecophylla smaragdina* (Hymenoptera, Formicidae) مبتنی بر تجزیه و تحلیل شواهد تبارشناسی و ژنتیک کمی وابسته به نظام اجتماعی

پ. پ. آناند*، ک.و. ماهیما و ی. شیوو واردانان*

بخش بیوشیمی و سم‌شناسی، گروه جانورشناسی، دانشگاه کلکته، کراالا، هند

* پست الکترونیک نویسندگان مسئول مکاتبه: anandpp633@gmail.com svardhanan@gmail.com

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چکیده: تشکیل نظام اجتماعی در حشرات و واگرایی ریختی ناشی از آن، به‌ویژه در مورچه‌ها هنوز به خوبی مطالعه نشده است. با این حال، اهمیت تلفیق ژنتیک و تکوین بر فرگشت موضوعی مورد مناقشه است. در این تحقیق، سعی کردیم تا واکنش‌های انتخاب ژنتیکی کمی، شواهد تبارشناسی و منشا فرگشتی طبقه افراد ماده (ملکه، کارگرهای کوچک و بزرگ) را رمزگشایی کنیم. افزایش پهنا و درازای ناحیه سر و زواید آرواره‌ای توسعه یافته، بارزترین خصوصیات توارثی یافت شده در کارگرهای بزرگ هستند. فرض بر این گرفته شد که این خصوصیات بی‌فرگشت و توارثی به این افراد مورچه‌ها برای دفاع، فرایند جستجوی غذا و دیگر عملکردهای لانه‌سازی کمک می‌کنند. اما در کارگرهای کوچک، سر کوچک و زواید آرواره‌ای تحلیل رفته، بیشتر جنبه توارثی دارند. در مقایسه با افراد کارگر، در مورچه ملکه خصوصیت بی‌فرگشت و توارثی بیشتر در ناحیه سینه و شکم بزرگ حشره، قابل تشخیص است. جالب توجه است که هیچ شواهد تبارشناسی در بین افراد ماده جمعیت مورچه بافنده آسیایی قابل شناسایی نبود. بر این اساس می‌توان استدلال نمود که توسعه نظام اجتماعی و واگرایی ریختی، پدیده حفظ شده فرگشتی نبوده و طی فرایندهای محیطی انسجام یافته‌اند. بر اساس نتایج این تحقیق، به این نتیجه رسیدیم که خصوصیات ریختی شامل شکل و اندازه مرتبط با طبقه اجتماعی، صفات بی‌فرگشت بوده و از ترجیح این حشرات در انتخاب آشیان اکوژیک منتج شده است.

واژگان کلیدی: ریخت‌سنجی هندسی، شواهد تبارشناسی، خصوصیات توارثی، واگرایی، مورچه‌های بافنده، نظام اجتماعی.