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Mandibular shape variation among different size classes of the ant *Camponotus sp.*(Hymenoptera: Formicidae)

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Abstract

This study was conducted to determine shape differences in the mandibles of different size classes of the ant *Camponotus sp.*. To do this, landmarks taken from digital images of a total of sixty minor (30) and major worker (30) ants were subjected to the outline-based Geometric Morphometric Analysis of Elliptic Fourier Analysis (EFA). Results showed global shape differences between the two types of worker ants. However, when mandibular shape was regressed with cephalic size, results indicate the negligible role that Allometry play in the disparity between the worker ants. This result suggest that polyethism in this species of ants is not dependent on age.

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Introduction

The shape of an organism can give information about how it moves (Losos, 1990), what it eats (Felley, 1984), and where it eats and lives (Douglas and Matthews, 1992). Moreover, size and shape are often related and these correlated traits have consequences for how taxa experience their environments (Kasparian and Weiser, 1999). Among the structures in living organisms that are well-studied in terms of size and shape characterization includes the mandible as it is believed to be a very important and vital structure for feeding. It also tells something about the feeding behavior of the organism.

Among invertebrates, the typical mandibular shape of ants is triangular with a smooth external margin and an internal masticatory margin with a variable number of teeth and denticles. In some species, mandibular shape has been modified to fit their proposed function (Wheeler, 1910; Bolton, 1994). Species of the genus *Polyergus*, an obligatory slave-making ant, has sickle-shaped mandibles to efficiently kill the opposing *Formica* in pupal brood raids (Trager and Johnson, 1985). The tribe Dacetini has evolved a mandibular trap mechanism referred to as trap-jaws (Gronenberg, 1996). The mandibles which are long, thin, and linear; with an apical fork of 2 or 3 spine-like teeth are held open awaiting prey (typically Collembola); when hairs are triggered the mandibles abruptly close and catch the prey (Gronenberg, 1996). In soldiers of *Eciton*, the mandibles are long and slim and they help in larvae transport during colony migration, as well as colony defence (Gotwald, 1995). Specimens from the Cephalotini tribe have short and thick mandibles that are used to dig chambers in tree trunks. In general, older individuals have smaller mandibles when compared to young individuals (Mayhe, 1994).

In most species, variability of such processes results in normal variation of body size and shape, but among a number of species of ants, selection for large differences in growth and relative growth has produced a worker caste that is greatly variable in

both body size and shape. This phenomenon is referred to as worker polymorphism and is present in about 15% of ant genera (Wilson, 1953; Oster and Wilson, 1978; Hölldobler and Wilson, 1990).

Species with extraordinary morphologies are also characterized by extreme variation in morphology, so that not all individuals express the trait to the same extent. Often, the exaggerated traits are expressed in only one sex, as, for example, in the case of the huge head and mandibles of soldier ant castes (all females) or the enlarged legs or horns in beetles (generally, all males). In addition, trait size often scales with body size, so that in a population individuals range from small, relatively normally proportioned animals, to very large animals with grossly enlarged structures.

Most measurable aspects of the insect body covary with body size (e.g. large flies have larger wings than small flies). When measurements are collected for large numbers of individuals of similar age or at the same life stage, it is possible to characterize the precise relationship between the dimensions of each trait and individual variations in overall body size (Emlen and Nijhout, 2000).

The cosmopolitan ant genus *Camponotus* Mayr (Hymenoptera: Formicidae) comprises 1584 described species (Bolton *et al.*, 2006). *Camponotus* is characterized by their mandibles and as described by General and Alpert (2012) is an extremely large genus in dire need of taxonomic revision which is a widespread genus in the Philippines. Twenty-eight species are presently known from the Philippines, but this is probably only a fraction of the total. This genus is unusual among formicines in that the usual conspicuous ring of hairs around the acidipore is absent. This genus can be recognized by the placement of the antennal insertions, which are always set back (not adjacent to) from the posterior clypeal border. *Camponotus* are often medium to large ants; dimorphic or polymorphic workers that forage along trails from their nest in wood. The distribution of

Camponotus species is patchy, influenced by soil types, vegetation and rainfall (Bolton, 1994). *Camponotus* differs from entire family of ants for its lack of metapleurall glands, a source of anti-bacterial secretions, except for some species such as *Camponotus thadeus* Shattuck (2004) of Australia and *Camponotus gigas* Latreille (1802) of Southeast Asia which possess this gland (McArthur, 2007).

Eusocial insects such as the *Camponotus* ant are known to have highly structured colonies where the organization of colony function is based on division of labor (Sirviö, 2010). Division of labor (when individuals within a group perform different roles) or polyethism comprehends a widely explored subject and may present two divisions: (a) physical polyethism, when individuals show distinct morphological characteristics to perform specific tasks and (b) temporal polyethism, when the variation of tasks occurs according to age (Wilson, 1971; Holldobler and Wilson, 1990). Therefore, temporal polyethism may occur both in populations of monomorphic workers and in polymorphic workers (Sudd and Franks, 1987; Sendova-Franks and Franks, 1999). Data for this species of ant still remains to be known. However, by studying closely the mandibular characteristics of this species, one can hypothesize whether this species undergo physical or temporal polyethism.

This study aimed to determine if mandibular shape differences and age polyethism are present between workers of the ant *Camponotus sp.* Age polyethism was based on size-dependent shape changes in the mandible from the study of Mantinget *al.* (2013) which used the out-lined based geometric morphometric analysis.

Materials and methods

Collection of ants

The collections of ant samples were mostly by handpicking. Ants seen crawling near the baits, under the logs or even on the dried leaves was directly handpicked while those arboreal ants by tapping the

twigs and directly placing them in a bottle of 70% ethyl alcohol. Digital photographs of collection of samples and the area were taken. Global positioning system, time, and habitat of the area were recorded.

Processing of the samples

Collected ant samples were brought to the Department of Biological Sciences laboratory for further processing. Each bottle of ant samples was sorted out using a fine forceps. Soil particles, tiny twigs and other dirt attached to their body were slowly removed. The sorted ant samples were selected such as major workers and minor workers before transferring them to another bottle of ethyl alcohol solution.

Ant samples were dry mounted on a clean paper. An examination of the 30 randomly selected major and minor worker ants was carried out using Leica (L350) Stereomicroscope at 30X magnification dissecting microscope. Digital photographs were taken with a Canon digital camera attached to the binocular microscope. Initial photographs of the full head view of the specimen were done to see important taxonomic characters in identification purposes. Each pair of mandibles was carefully dissected using fine forceps and was then photographed. Dissected mandibles were placed in a labelled eppendorf tubes for further analysis.

Morphometric analysis

To explore whether there was a relationship between the ant size and mandibular shape of the collected *Camponotus* ant species, Cephalic Index of the ant species were measured. Up to thirty specimens from the collected ants were measured.

Measures of cephalic index are frequently used as indices of overall size, and are frequently used in ant taxonomy. Two measures of head size were taken: maximum head length in full face view – occipital margin to clypeus – exclusive of teeth, spines, or tubercles and head width in full face view exclusive of eyes (Weiser and Kaspari, 2006).

Outline analysis

Principal components analysis (PCA) on morphometric measurements (Jolliffe, 2002; Weiser and Kaspari 2006) provides the means to summarize the size and shape of ant specimens and construct a “morphospace” (Pie and Traniello 2007) where morphological associations can be displayed and used for analysis (Danoso and Ramon, 2009). PCA was used to construct an ant community morphospace using Cephalic Index. The analysis was performed using PAST (Paleontological statistics, version 2.14). Measurements were transposed from which principal component (PC) scores were extracted with Jolliffe cut-off.

Outline-base analysis was used to analyze the shape of the internal and external margins of the mandible. TpsDig ver. 2 software was used to allow points on the image and transforming the data into thin plate spline making constant of the non-shape in order to remove the non-shape variation (Dela Cruz *et al.*, 2011) acquiring a total of 100 points. The x and y coordinate

of the one hundred points outlined from the mandibles were subjected to Elliptic Fourier Analysis (EFA). Further analysis used is the Paleontological Statistics software (PAST) version 2.14 to provide a way to reduce complex data into simple dimensions that reveals simple structures (Shlens, 2005).

Results and discussion

Global variation in the shapes of the mandible

Overall variation in the shapes of the left and right mandibles between minor and major workers was determined via discriminant function analysis (Fig. 1). Results showed differences in the shapes of the mandibles between the two, which is indicative of character displacement resulting from possible differences in their functional roles in the nest. The major workers in this species act defensively whenever there are threats to the ant colony. This might explain why they differ in terms of mandibular shape from the minor worker ants. The latter takes care only of the brood and of the nursery, thus explaining their unique mandible shape.

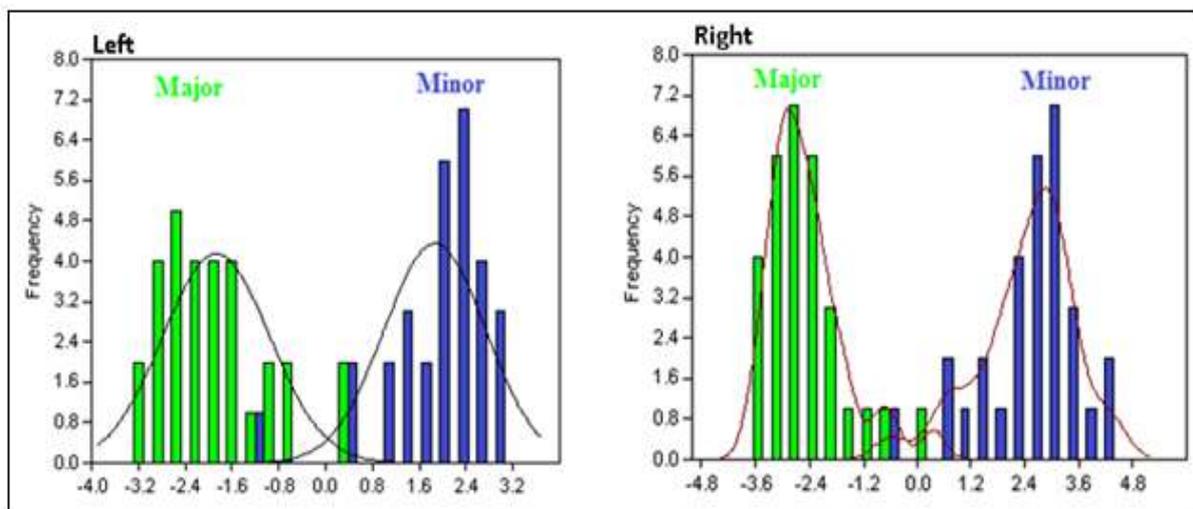


Fig. 1. Frequency histograms showing shape differences in the mandibles between minor and major worker ants.

Localized variation in the shape of the mandible

The size and shape components of the mandible of the ants were analyzed to determine patterns of variability that can be used to infer allometry in mandible shape. The shape components were decomposed into local shape variations in the form of principal component scores derived from the analyses

of the Procrustes-fitted landmarks. The size component used was the cephalic index which is the ratio between the length and the width of the head. Both the size and shape components were then analyzed using correlation analysis to determine allometry. The results are presented in fig.1 and 2.

In general, variability in the shapes of the mandibles was described using a total of six principal components for each of the mandible totalling to twelve. The first principal components explain most of the variation and explain 56.69% and 50.80% of

the variance for the right and left mandibles, respectively. The second principal components explain only 11.60% to 15.19%, while the rest capture less than 9% variance.

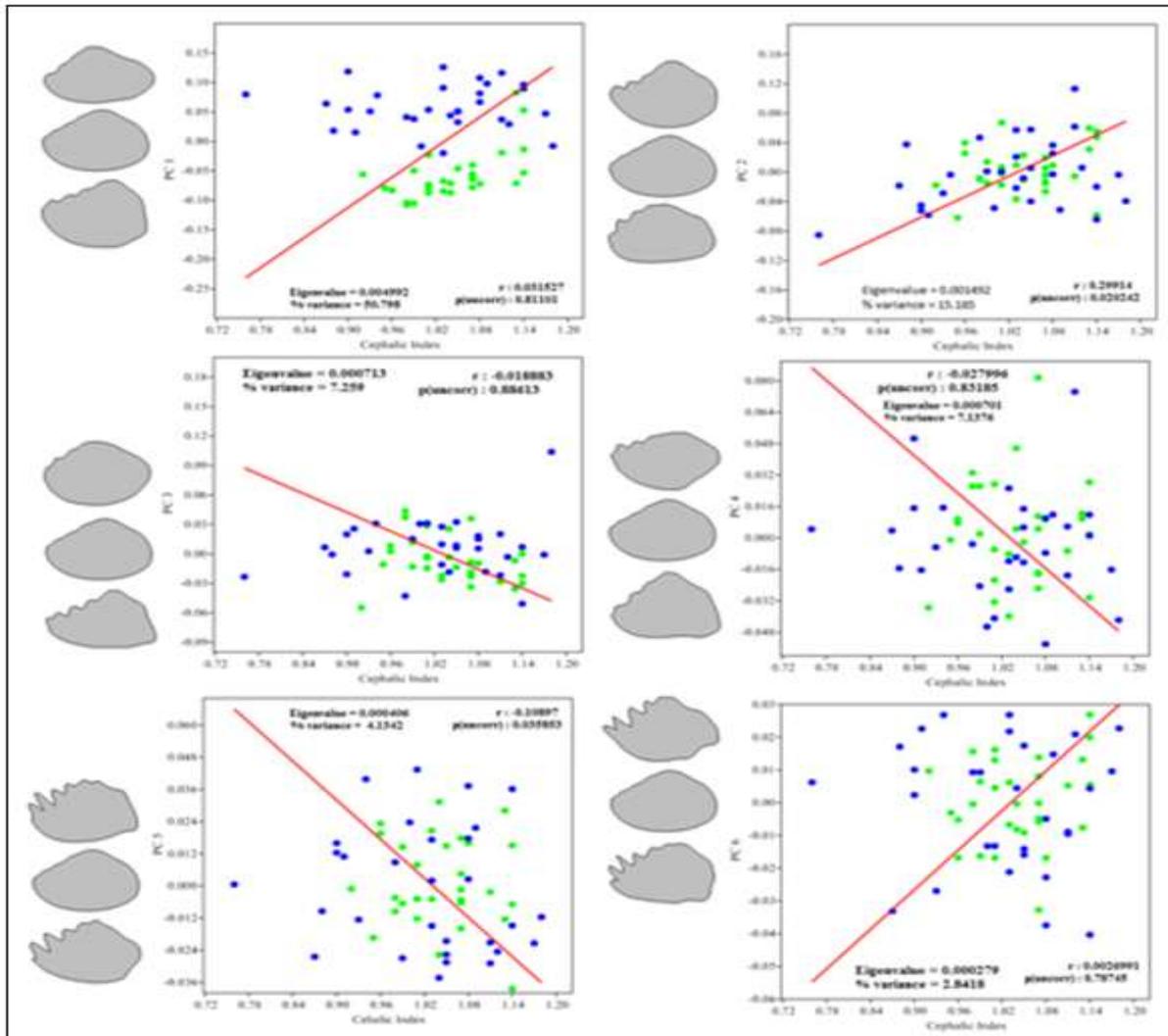


Fig. 2. Results for the test of the size dependent shape changes in the left mandible of *Camponotus* sp. Legend: Blue – Minor Workers; Green –Major Workers.

For the left mandible, the shape of the mandible was decomposed into six principal components and tested for correlation with cephalic index. Correlation analysis failed to determine significant relationships between the first, third, fourth, and sixth principal components and the cephalic index. However, significant correlations were detected between the second and fifth PCs and cephalic index. Looking at the latter PCs, the results also showed overlaps

between the plots of both the minor and major workers. This result might imply that ontogeny might not produce patterns of size-shape relationships in the mandible of both groups of worker ants.

For the right mandible, significant correlations were shown in the second, fourth and fifth PCs and cephalic index. The head shape changes with body size, but the relative size of the mandibles to the body

does not. The relationships between the mandible size and shape show that the first component explains 56.6% of the variation in shape, and represents a species which have either narrow (negative scores) and those with rounded or more robust mandibles

(positive scores). The rest of the principal components explain localized variations especially on the shapes of the denticles. Moreover, variability can be seen in the shapes of the basal angles and the apical tooth.

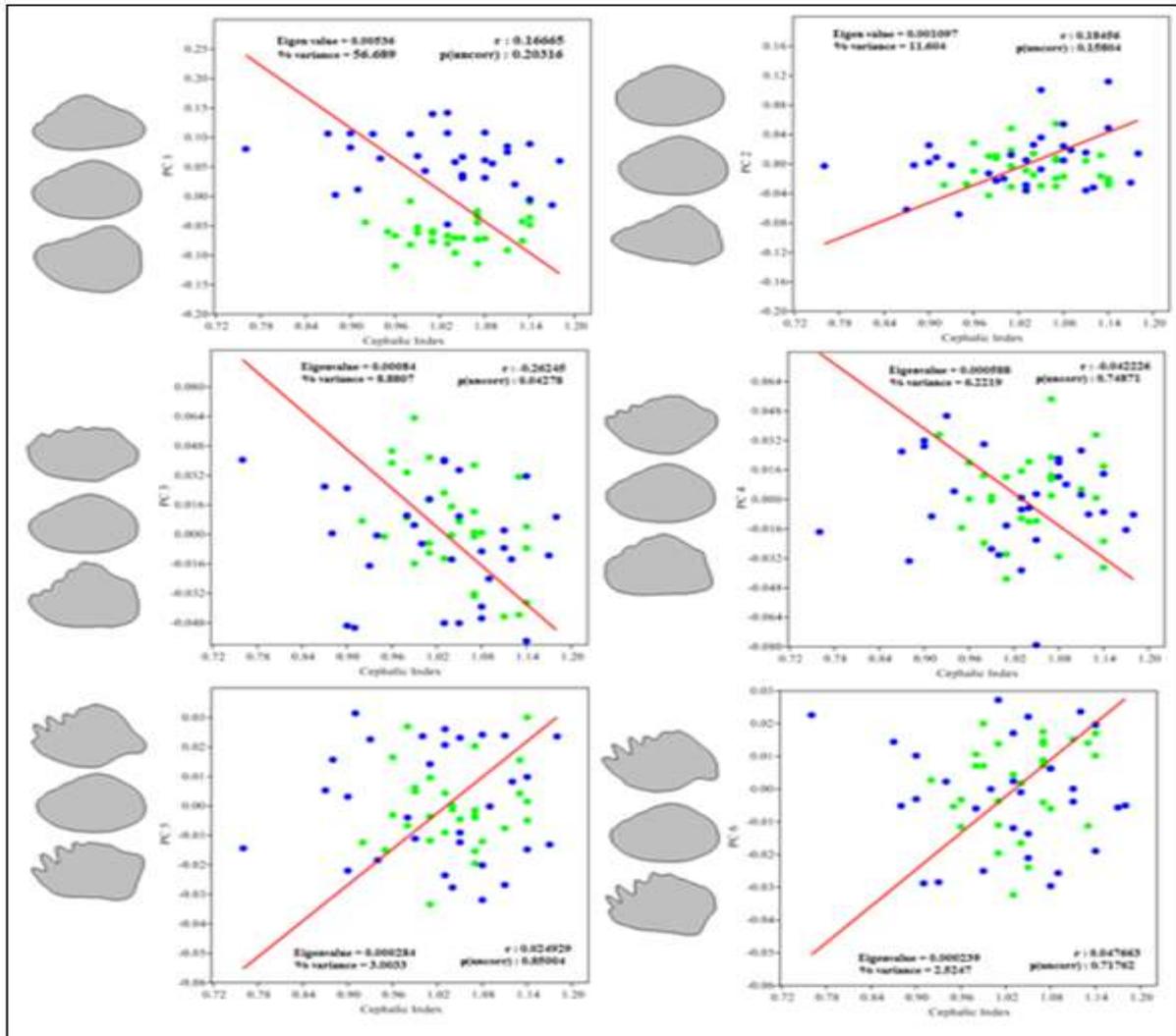


Fig. 3. Results for the test of the size dependent shape changes in the right mandible of *Camponotus* sp. Legend: Blue – Minor Workers; Green –Major Workers.

While age-dependent polyethism does not explain differences in the shapes of the mandibles of minor and major worker ants in *Camponotus* sp., it nonetheless has been detected in other species of ants such as *Diacamma rugosom* (Manting et al., 2013) and three species of *Odontomachus* namely *O. bauri*, *O. Infandus* and *O. Simillimus* (Manting et al. 2015). Such fixation in the ants role in the colony can also be observed in other species of organisms including

wasps. Yet, an explanation to such phenomenon is still to be explored.

Conclusion

The results of this study showed the absence of temporal polyethism in this species of ant. This tells us that the minor and major ants might already have differed in the shapes of their mandible as soon as

they are born and that these differences might also explain differences in their roles in the colony.

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