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Mandibular shape variation among size classes in the worker ants of *Pheidologeton diversus*

Mark Anthony J. Torres*, Eugene Vernon V. Tañedo Jr.

Department of Biological Sciences, Mindanao State University- Iligan Institute of Technology, Philippines

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Abstract

The geometric morphometric approach of landmark analysis was utilized in this study to compare the shapes of the mandibles of three size classes of the ant *Pheidologeton diversus*. To do this, the X and Y coordinates of a total of fifty points were digitized and subjected to relative warp analysis. Results showed that the mandibular shapes of the smaller-sized ants differed significantly from those of the medium- and larger-sized classes. The observed differences can be related to the presumed roles that the ants play in their colonies.

*Corresponding Author: Mark Anthony J. Torres ✉ markanthony@gmail.com

Introduction

Differences in the morphological attributes of eusocial ants are said to facilitate task variation among members of the colony (Holldobler and Wilson, 1990). In the species *Pheidologeton diversus* for example, males belonging to several size classes are known to perform different roles in the caste. In the colony, smaller and younger males with lengths from 1.3-2.5 mm are assigned to care for the larvae. These ants, which are called minor workers, are assigned new tasks as soon as they grow. As time passes, each minor worker transitions to become major worker ants whose role is to forage and collect food for the colony. Ontogeny does not stop among the major worker ants as they continue to grow further to become soldier ants whose function now includes protecting the colony from harmful invaders and predators aside from its foraging activities (Holldobler and Wilson, 1990).

The ontogenetic change in the body sizes of the ants described above is accompanied by differentiation in the characteristics of the mandible. When the minor workers are still young, they possess sharper mandibles that have five “teeth”. These teeth slowly disappear as individuals grow older. Upon reaching the “major worker” stage, the mandible of the ants then assume a triangular shape with a characteristic acute basal angle. As worker ants use their sharp mandibles every day, it gradually gets dull and blunt as time passes with each work done. Not only will the physical appearance of the ants change but their eating habits as well. Since chewing will inevitably become a problem for worker ants with duller mandibles, older workers are only able to squeeze-out the juice from their food then throw the dried up part (Wheeler and Bailey, 1920). In the final transition towards being a soldier ant, the mandibles hardened into a tool for defense (Holldobler, and Wilson, 1990). This hardness of the feeding apparatus is said to be a function of the concentration of zinc in the mandible (Schofield, 2002).

In this study, the ontogenetic changes in the

morphological attributes of worker and soldier ants belonging to *Pheidologeton diversus* are described using the tool of geometric morphometrics, specifically out-line based analysis.

Materials and method

Collection of samples

Ant samples were collected from a nest at the Initao National Park in Misamis Oriental, Philippines. During the conduct of the sampling, a trail of *Pheidologeton diversus* that was leading towards its colony were amassed and preserved in a 70% ethyl alcohol solution. Before dissecting the mandibles out from the bodies, the ants were grouped into three size-classes. These size classes reflect their natural grouping in the environment. The smallest were regarded as minor workers, mid-sized ants as major workers and the larger ones as soldiers. The picture in figure 1 shows how easy it was to group the ants into the three size categories. When extracting the mandibles, the feeding apparatus were opened wide until the base of the structure detaches from the mouth.

Digitization of landmark points

Images of the left and right mandibles were taken using a camera mounted on top of a stereo microscope. The images were then processed using the software TPS utilities by Rolf (2003) and the outlines of the mandibles were traced by manually digitizing a total of fifty landmarks from around the structure (Fig. 2). These landmarks were intentionally collected to provide information on the shapes of the basic parts of the mandible (Fig. 3).

Outline-based geometric morphometric analysis

The algorithm employed in the analysis, which is called elliptic fourier analysis (EFA), was used to reconstruct the shapes of the mandibles. This was done separately for both the left and right mandibles. Aside from generating reconstructed images, the EFA analysis also returned numerical coefficients that were further used as multivariate variables.

Statistical analyses

The EFA coefficients were then subjected to the ordination method called principal component analysis to determine similarities in the shapes of the mandibles of the three size classes. The results of the analyses were then depicted as scatter diagrams where polygons were used to define the extent of mandibular shape variation among size classes. The same coefficients were also subjected to multivariate analysis of variance (MANOVA) to test for significant differences between the groups. All analyses were conducted using the PAST software as platform

(Paleontological Statistics software by Hammer and Harper).

Results and discussion

The reconstructed shapes of the mandibles are shown in fig. 4. Results showed variations in the outlines of the feeding apparatus from having a sharp appearance in the positive PC1 axes to a more robust but duller one in the negative PC1 axes. Also noteworthy to mention are the small protrusions in the internal margins of the reconstructed +PC1 mandibles, which might be indicative of the presence the of teeth.

Table 1. Pair-wise comparison showing significant differences in the shapes of the mandibles between the small-sized worker and the other size-classes. Legend: Upper triangle – left mandibles; lower triangle – right mandibles. Permutation: 10,0000.

	Minor Workers	Major Worker	Soldiers
Minor Workers		0.0020	0.0015
Major Workers	0.0180		0.9665
Soldiers	0.0009	0.2153	

The second principal component axes on the other hand, describe differences in the shapes of the basal part. The other PC axes describe some protrusions in the mandibular margins. Another thing that can be noticed from the figure is the dissimilar pattern

between the reconstructed left and right mandibles. This might be an indication of the phenomenon called fluctuating asymmetry, which has recently been described in bilateral structures.



Fig. 1. Diversity of sizes of the *Pheidologeton diversus*.

The results in fig. 5 and table 2 answers questions pertaining to whether the size-classes of worker ants and soldiers differ in the shapes of their mandibles. The figure tells of differences in the mandibles especially with when the right sides were compared. Also, based on the diagram, the yellow polygon representing the soldiers appears to occupy a different space in the two-dimensional space.

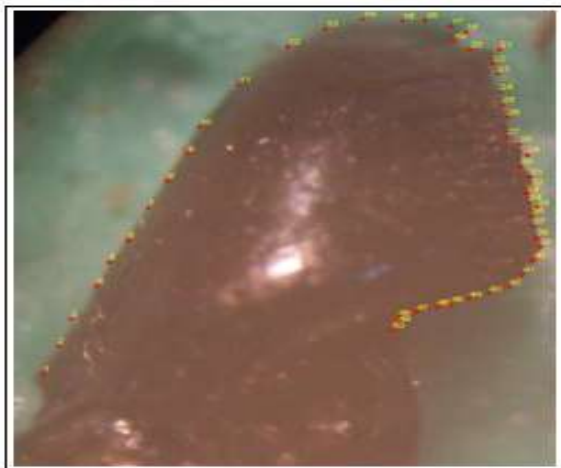


Fig. 2. Positions of a total of fifty landmark points which were manually digitized from the mandibles of the worker ants.

This reinforces the observation that soldiers differ from the younger minor and major workers in having blunt and dull mandibles already because of wear and tear. This result is also supported by the results of the multivariate analysis of variance (MANOVA) which detected significant differences in the shape coefficients between the size classes.

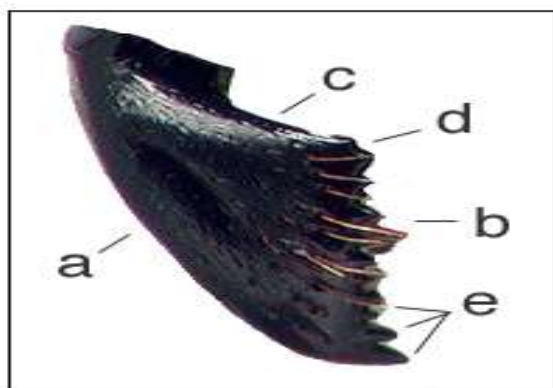


Fig. 3. Basic parts of an ant's mandibles are being shown. With a: being the external margin, and b-e: being the internal margin: b: masticatory margin; c: basal margin; d: basal angle; e: teeth.

Although mandibular shapes have been established for the three different groups, a thorough assessment of the extent of morphological differentiation can also be studied across colonies of the ant.

In a study by Geraghty *et al.* (2007), the size of the colony and its range are also said to affect the body sizes of the ants. Moreover, elevational gradients have also been presented as one of the more influential factor. In a detailed study conducted by Borgo *et al.* (2013), biochemical agents important in mate recognition reinforce the existing the genetic and morphological differentiation of the colonies.

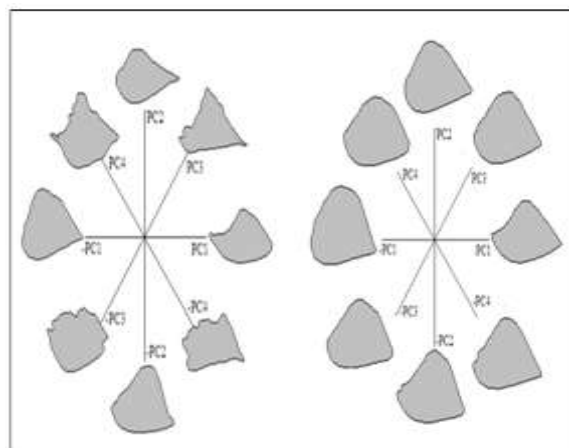


Fig. 4. Possible mandible shapes of the right (left side) and left (right side) mandibles.

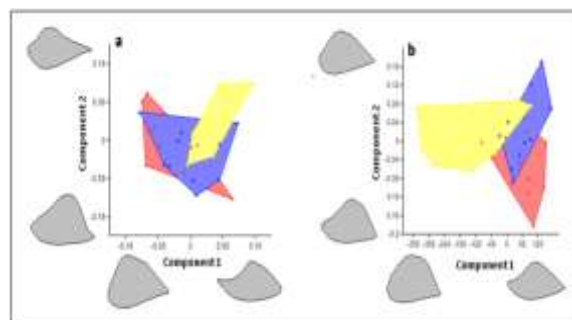


Fig. 5. Mandibular shape variaion among three size classes of *Pheidologeton diversus*. Legend: (a) left and (b) right mandibles. Legend: Red- minor workers; Blue – major workers; Yellow- Soldiers.

The result herein presented not only describes the patterns of morphological differentiation in a structure that is of functional significance to ants (Gronenberg, 1995) but also bespeaks of the utility of

Geometric Morphometrics in recreating outlines of two-dimensional biological structures of organisms. This has been proven useful already in other related studies (Torres, 2013).

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