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Mandibular Shape Variation in the Three Species Of *Odontomachus* Latreille 1804 (Hymenoptera: Formicidae)

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ABSTRACT

This study was conducted to determine shape differences in the mandible among the workers of the eusocial ant Odontomachus. The mandible is used by the ant to kill or maim preys to be brought to the nest or simply lock and snap its jaws if one bite is not enough, or to cut off bits of larger food. The mandibles also permit slow and fine movements for other tasks such as nest building and care of larvae. Because of the so many functions of the mandible, changes in its morphology may differ within and between species thus this study was conducted. Morphological wear could occur in the mandibles which can be quantitatively measured using imaging, shape geometry and multivariate statistical tools. In this study a comparison was made between workers of the three species. A total of 30 worker ants per species were examined where the outlines of the left and right mandibles were digitized and the coordinates were subjected to Elliptic Fourier analysis (EFA). The resultant shape variables were then analyzed using Principal Component Analysis (PCA) and the shape variations described for the three species. Results showed no continuous allometric size variation, but significant shape differences were found between the mandibles of the three Odontomachus species which can be correlated to their morphological functions and constraints.

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INTRODUCTION

The ponerine ant of the genus *Odontomachus* most conspicuous feature is the trap-jaws which can be opened to an angle of 180^0 and close in less than 0.5 mm [1]. The large linear mandible attached very near each other at the middle of the oral margin of the head can be closed extremely rapidly to trap, kill or maim the prey [2] allowing them to be brought to the nest. The mandible can be simply locked and snapped if one bite is not enough, or can be used to cut off bits of larger food. It can also permit slow and fine movements for other tasks such as nest building and care of larvae [3]. Because of these numerous functions, variations in the mandible may happen and can be observable within the species or between species. It may also be possible that a different kind of worker ant can have a different kind of mandibular shape brought about by what is known as polyethism, a division of labor among the ants due to differences in functions in a caste or the difference over time is due to aging [4]. Mandibular wear may also be a major factor for the differences and will be observable with a careful quantitative description of the mandibular structure. In this study therefore, we quantitatively describe the mandibular shapes of three species of *Odontomachus, O. bauri*, *O. infandus,* and *O. simillimus* to be able to understand possible causes of variations in the mandible if there are any, using Geometric morphometric analysis that has been used to quantify differences in biological shapes [5]. In the study, allometric shape variation and identification of the presence or absence of age polyethism in the mandibles among three species of the worker ant *Odontomachus* were also addressed.

Methodology:

Individuals of the three ant species were collected from the municipality of Malabang, Lanao del Sur, Initao, Misamis Oriental and New Corella, Davao del Norte, Philippines. Body size measurements of the

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workers were measured from the maximal outer orbital distance and the head length from the posterior margin of the head to the apex of clypeus [6] [7].

Specimens were stored in 70% ethyl alcohol solution [7] and brought to the laboratory in preparation for imaging. Mandibles were dissected from 30 randomly selected worker ants from each species, mounted in a clean glass slides, covered and photographed using Leica Stereomicroscope L350 at 30X magnification dissecting microscope (Fig. 1).

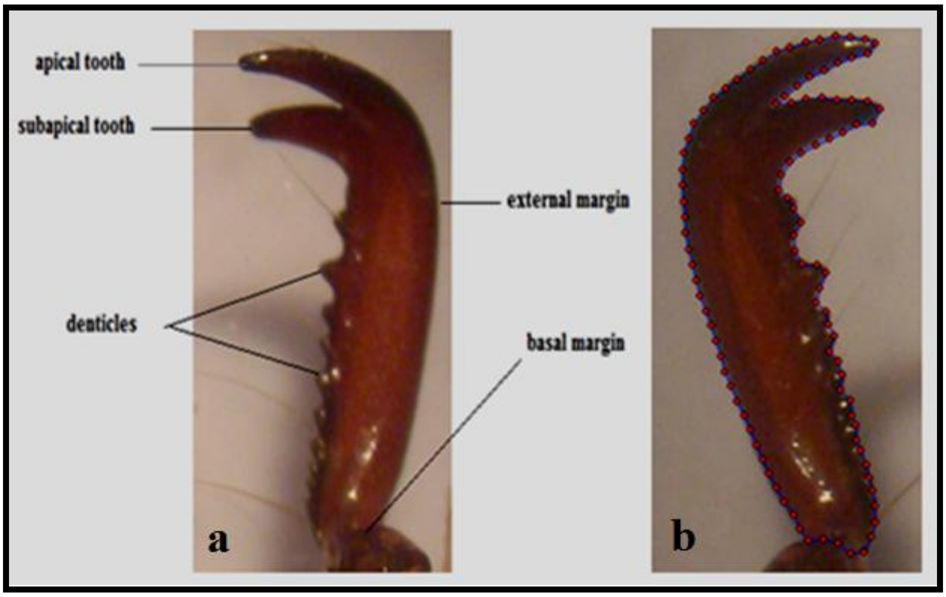

Fig. 1: External mandible morphology (a) Dorsal view and (b) Position of 100 outlines points in the mandible.

For the shape analysis of the mandibles a total of 100 points were digitized from the left and right images of the mandibles using TpsDig ver. 2.12 [8]. These points covered the internal and external margins of the mandible. These include the masticatory margin, basal margin, and mandulus. The X and Y coordinates of the outline points were saved in Matlab format and were subjected to Relative Warp Analysis to remove non-shape components using TpsRelw ver. 1.46 [9]. Using the thin-plate spline equation and the standard formula for uniform shape components, a weight matrix (containing uniform and non-uniform shape components) from the aligned specimens were generated. The RW scores and morphometric measurements were then subjected to Multivariate Analysis of Variance (MANOVA) to test for shape differences in mandible topology in the three species of *Odontomachus* using the PAleontological Statistics software, version 2.13 [10].

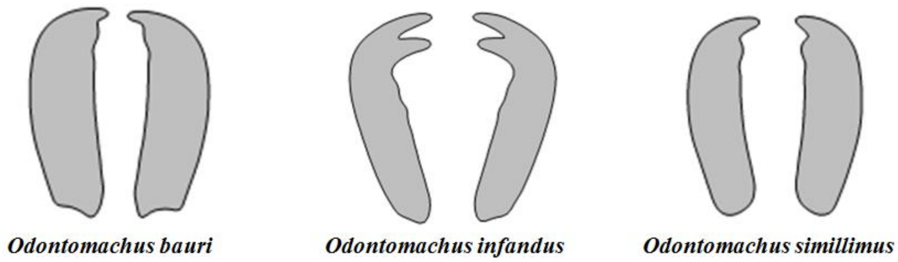

Fig. 2: Mean mandible shape of the three species of *Odontomachus*.

RESULTS AND DISCUSSION

Qualitative description of the mandibles shows *O.bauri* has long and short mandible that has short, emarginated to round, acute, and subapical tooth with blunt to absence of denticles in masticatory margin, emarginated basal margin nd with acute to wide acute basal angle. *O. infandus* has mandibles that are long and slender with long and round to acute apex and subapical teeth, occasionally the apical tooth is much longer than subapical tooth or apical tooth is slightly shorter than the subapical tooth, The masticatory margin with has prominent 1st and 2nd denticels with teeth apex varies from acute to round and sometimes blunt or absence of denticels. The basal margin varies from emarginated, truncate or rounded with acute to obtuse basal angle. *O. simillimus* has narrow mandibles, slightly elongated apical tooth with acute to rounded apex. The Subapical tooth is short with emarginate to round margin, has blunt to rarely visible denticels in the masticatory margin and with truncate to round basal margin with obtuse basal angle (Fig. 2).

Quantitative analysis of the shapes of the three species of *Odontomachus* shows distinctness of their mandibles (Fig. 3). Canonical variate analysis indicate highly significant differences between species for both the left and right mandibles (Fig. 3, Table 1 and 2).

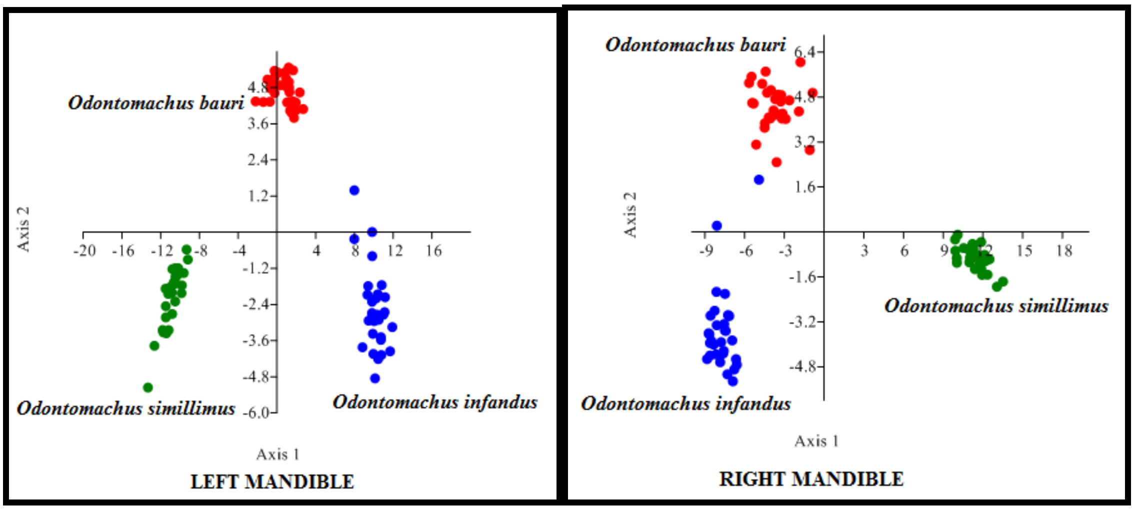

Fig. 3: MANOVA/CVA Plots of the first two principal components explaining differences in shapes of the mandibles among the three species of the worker ants of *Odontomachus*.

Table 1: Canonical variates analysis of Principal Components.

Left Mandible	Wilks' lambda	df1	df2	F	p-value
	0.00152	8	168	626.4	8.11E-121
	Pillai trace	df1	df2	F	p(same)
	1.906	8	170	430.8	1.30E-108
Right Mandible	Wilks' lambda	df1	df2	F	p(same)
	0.001138	8	168	601.6	2.15E-119
	Pillai trace	df1	df2	F	p(same)
	1.905	8	170	426.8	2.76E-108

Table 2: Pairwise comparison of the shapes of the mandibles of the ant workers of the three species of *Odontomachus*.

LEFT/RIGHT Mandible	*O. bauri*	*O. infandus*	*O. simillimus*
O. bauri	-	1.20E-42	2.77E-45
O. infandus	2.47E-37	-	6.46E-56
O. simillimus	1.03E-46	2.37E-55	-

Note: significant value $p < 0.05$.

Reports on similar studies conducted on *Pheidologeton diversus* found significant allometry and size-dependent variation of the shapes of the mandible [11]. These variations observed were explained as resulting from the differentiation of the worker ants into different size classes as (a) minor workers, (b) major workers and (c) supra major workers with each size class having distinct shape and size of the mandible. In this species therefore, there is a relationship between mandibular size and shape and the ants' role in their colony.

Linear regression analysis of the three species of Odontomachus:

Results of the linear regression analyses to determine if there is a relationship between body size index and mandibular shapes for the three species are presented in the figures 4 – 9 and table 3. The findings show no significant relationship between body size index and mandible shape signifying the absence of size-dependent allometric variation in the species of *Odontomachus* ants. Although no size-dependent variation was observed, the results showed variation within species in the shapes of the mandible as shown by the distribution of the points representing individual ants in the scatter plot (Figures 4-9). The variations observed are summarized in Tables 4 and 5. The observable variations in the shapes of the mandibles are on the number of denticles, length of teeth, the angle of the basal angle, length of the protrusion of the first and second teeth, distance of the teeth between each other, and the angle of connection between the masticatory margin and the first tooth from the external margin.

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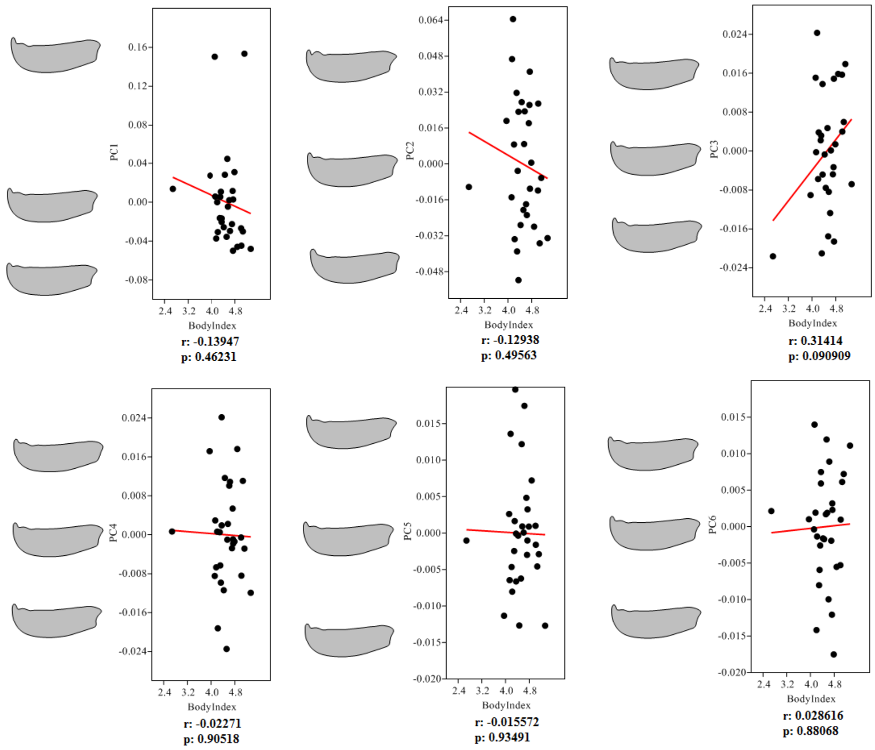

Fig. 4: Linear regression showing the correlation between the body size and the left mandible shapes of *O. bauri* workers.

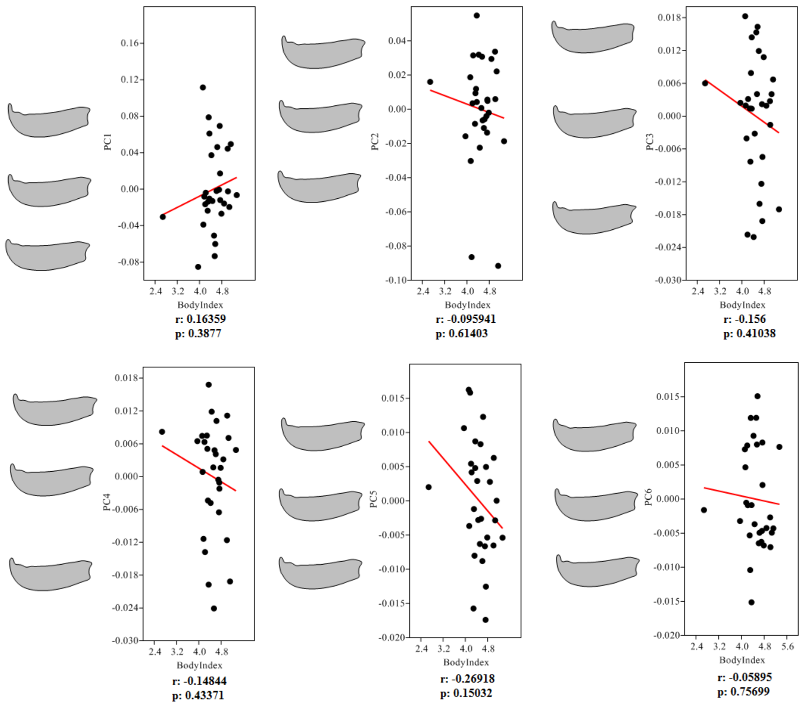

Fig. 5: Linear regression showing the correlation between the body size and the right mandible shapes of *O. bauri* workers.

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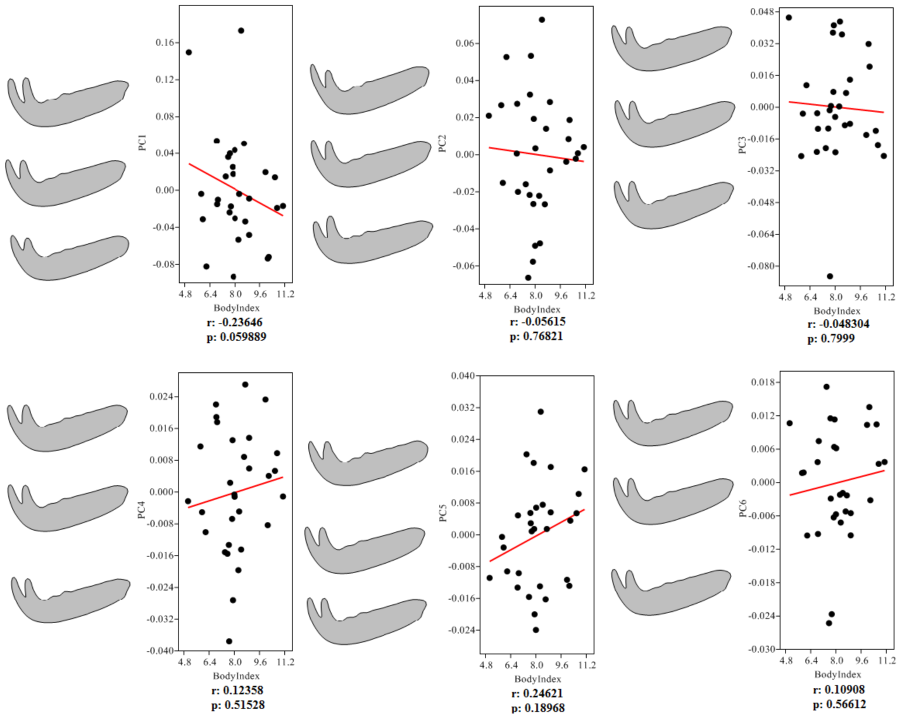

Fig. 6: Linear regression showing the correlation between the body size and the left mandible shapes of *O. infandus* workers.

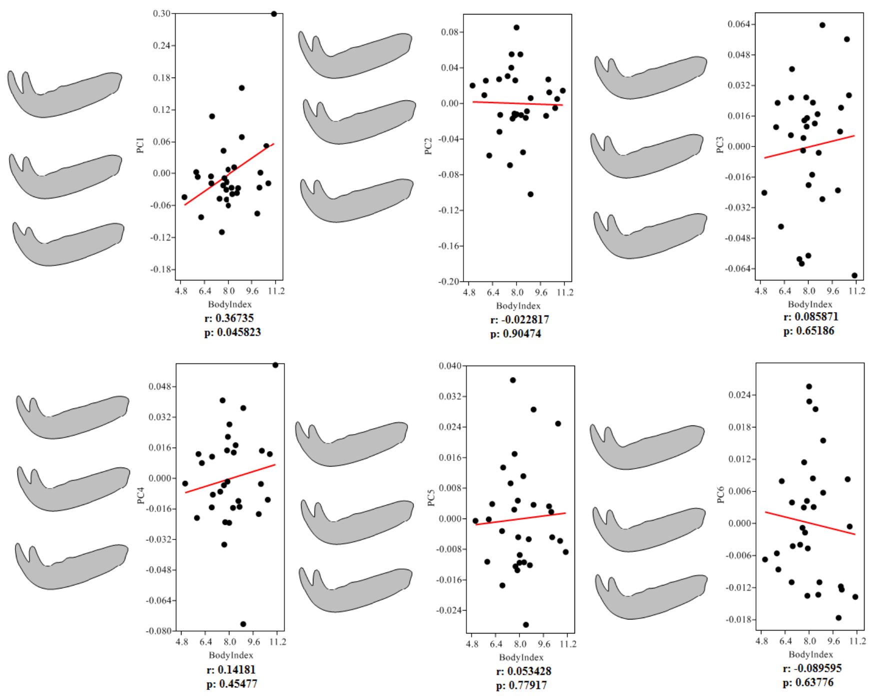

Fig. 7: Linear regression showing the correlation between the body size and the right mandible shapes of *O. infandus* workers.

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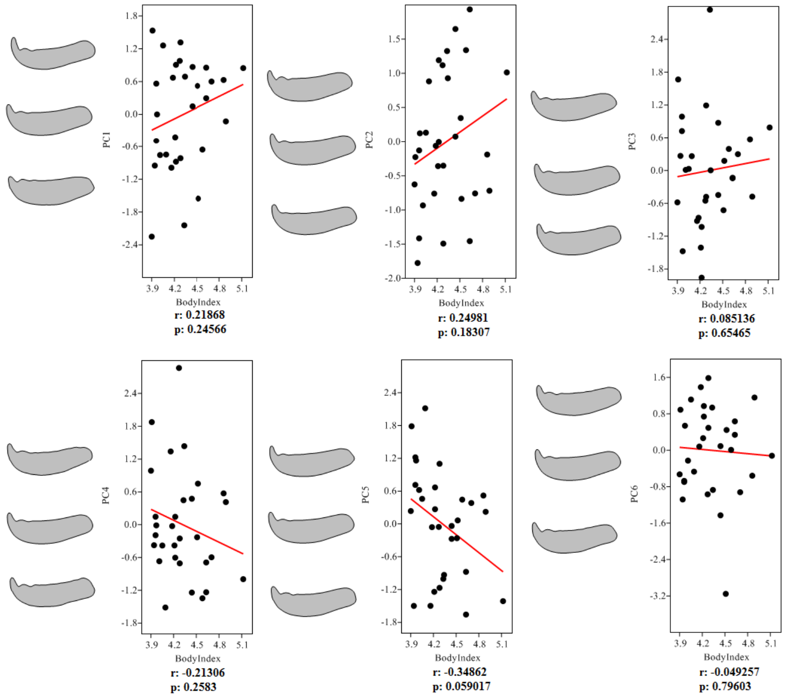

Fig. 8: Linear regression showing the correlation between the body size and the left mandible shapes of *O. simillimus* workers.

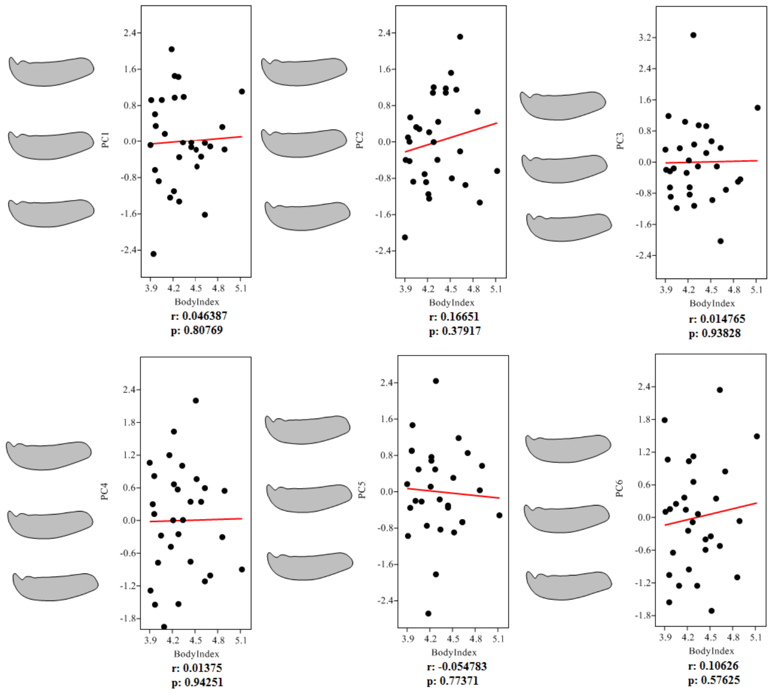

Fig. 9: Linear regression showing the correlation between the body size and the right mandible shapes of *O. simillimus* worker ants.

Table 3: Correlation analysis of the relationship between Mandible shapes and Body Size Index.

Odontomachus bauri						
	Left Mandible			Right Mandible		
	Slope	r	p	Slope	r	p
PC1	-0.014046	-0.13947	0.46231	0.015393	0.16359	0.3877
PC2	-0.0077591	-0.12938	0.49563	-0.0061606	-0.95941	0.61403
PC3	0.0078693	0.31414	0.090909	-0.0036533	-0.156	0.41038

PC4	-0.00049936	-0.02271	0.90518	-0.0031069	-0.14844	0.43371
PC5	-0.00025685	-0.015572	0.93491	-0.0048063	-0.26918	0.15032
PC6	0.00045224	0.028616	0.88068	-0.00091264	-0.05895	0.75699
Odontomachus infandus						
	Left Mandible			Right Mandible		
	Slope	r	p	Slope	r	p
PC1	-0.0093235	-0.23646	0.20837	0.019334	0.36735	0.045823
PC2	-0.0012391	-0.05615	0.76821	-0.0005941	-0.02282	0.90474
PC3	-0.00087527	-0.048304	0.7999	0.0019352	0.085871	0.65186
PC4	0.0012716	0.12358	0.51528	0.002445	0.14181	0.45477
PC5	0.0021731	0.24621	0.18968	0.00050324	0.053428	0.77917
PC6	0.00073426	0.10908	0.56612	-0.00069537	-0.0896	0.63776
Odontomachus simillimus						
	Left Mandible			Right Mandible		
	Slope	r	p	Slope	r	p
PC1	0.68661	0.21868	0.24566	0.14565	0.04639	0.80769
PC2	0.78437	0.24981	0.18307	0.52281	0.16651	0.37917
PC3	0.26731	0.085136	0.65465	0.04636	0.01477	0.93828
PC4	-0.66896	-0.21306	0.2583	0.04317	0.01375	0.94251
PC5	-1.0946	-0.34862	0.059017	-0.17201	-0.05478	0.77371
PC6	-0.15466	-0.049257	0.79603	0.33365	0.10626	0.57625

The source of the variations observed within the three species indicate mandibular wear but goes independently with body size, thus there is no age polyethism within the worker class. Similar observations were made in *Formica yessensis,* where the aging workers has more worn out mandible since it has repetitive work [4][6] since there is lack of temporal-related division of labor in this group of ants suggesting that they do not have age-based task-switching. Such fixation in their job was also documented in wasps and some species of ants [12][13][14]. One of the major reasons not to change preferences in their work is due to overwhelming positive stimulus such as that in *Amblyopone pallipes* where a positive feedback like starving larvae due to the lack of supply of food makes them affixed to one type of work [15]. Furthermore, other ants comprised of only small number of entities would have less number of individuals that would forage for food to support their colony thus stability in their work is a more preferred option.

Conclusion and recommendation:

The correlation between mandibular shape and body size index in *O. bauri*, *O. infandus* and *O. simillimus* showed no age polyethism and age-based task switching were observed within the worker class. The variations within species that were observed can be attributed to mandibular wear considering that the worker ants are fixed to their specific tasks of food gathering, nest building and repair.

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Table 4: Percentage of variance and overall shape variation in the left mandible as explained by each of the significant principal components of the three species of *Odontomachus.*

LEFT MANDIBLE						
PC	% Variance	*Odontomachus bauri*	% Variance	*Odontomachus infandus*	% Variance	*Odontomachus simillimus*
1	63. 60	Apex of the apical tooth slightly elongated, rounded and blunt. Short, truncate subapical tooth of mandible with blunt masticatory margin to absence of denticles. Basal margin emarginate with obtuse-acute basal angle.	55.44	Mandibles long, with long rounded apical and subapical teeth with prominent acute1st and 2nd teeth in the masticatory margin to mandibles with short apical and subapical teeth with blunt first two dentition in the masticatory margin. Basal margin emarginate-round with acute-wide obtuse basal angle.	53.92	Mandibles narrow with apical tooth long to slightly elongated, rounded and blunt apex. Short, rounded subapical tooth with blunt masticatory margin to absence of denticles. Basal margin rounded-emarginate with obtuse basal angle.
2	22.56	Apex of the apical tooth slightly elongated, rounded and blunt. Short, rounded and blunt to absence of subapical tooth and denticles in the	17.37	Mandibles long, with longer rounded apical and shorter subapical teeth with prominent acute1st and 2nd teeth in the masticatory margin to mandibles with	26.58	Mandibles narrow with apical tooth long to slightly elongated, acute-rounded and blunt apex. Short, rounded subapical tooth with blunt

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		masticatory margin of mandible. Basal margin emarginate with narrowly acute to obtuse basal angle.		shorter apical tooth than subapical tooth with blunt first two dentition in the masticatory margin. Basal margin truncate with obtuse basal angle.		masticatory margin to absence of denticles. Basal margin rounded with obtuse basal angle.
3	3.94	Slightly elongated, rounded to acute apex of the apical tooth. Short, truncated and blunt subapical tooth of mandible and blunt masticatory margin and absence of denticles. Basal margin emarginate with obtuse basal angle.	11.71	Mandibles long, with shorter subapical tooth than apical tooth with rounded-acute 1st and 2nd teeth in the masticatory margin to mandibles with long apical tooth than subapical tooth with blunt first two dentition in the masticatory margin. Basal margin truncate with obtuse basal angle.	6.95	Mandibles narrow with apex of the apical tooth long to slightly elongated, rounded and blunt apex. Short, rounded subapical tooth with blunt masticatory margin to absence of denticles. Basal margin rounded with obtuse basal angle.
4	3.03	Slightly elongated, rounded to apex of the apical tooth. Short, truncated - rounded and blunt subapical tooth and absence of denticles in the masticatory margin. Basal margin emarginate with obtuse-acute basal angle.	3.78	Mandibles long, with slightly shorter subapical tooth than apical tooth with rounded-acute 1st and 2nd teeth in the masticatory margin Basal margin truncate with obtuse basal angle.	2.31	Mandibles narrow with apical tooth long to slightly elongated, rounded and blunt apex. Short, rounded subapical tooth of mandible with blunt masticatory margin to absence of denticles. Basal margin rounded-truncate with obtuse basal angle.
5	1.71	Slightly elongated, acute-rounded apex of the apical tooth. Short, truncated - rounded and blunt subapical tooth and absence of denticles in the masticatory margin. Basal margin emarginate with acute-obtuse basal angle.	2.78	Mandibles long, with slightly shorter subapical tooth than apical tooth with rounded-wide acute 1st and 2nd teeth in the masticatory margin Basal margin rounded-truncate with obtuse basal angle.	1.97	Mandibles narrow with apical tooth long to slightly wide-elongated, acute-rounded and blunt apex. Short, rounded subapical tooth of mandible with blunt masticatory margin to absence of denticles. Basal margin tuncate-rounded with obtuse basal angle.
6	1.57	Slightly elongated, rounded to apex of the apical tooth. Short, truncated - rounded and blunt subapical tooth and absence of denticles in the masticatory margin. Basal margin emarginate with obtuse-acute basal angle.	1.62	Mandibles long, with slightly shorter and wide subapical tooth than apical tooth with rounded-acute 1st and 2nd teeth in the masticatory margin Basal margin truncate with obtuse basal angle.	1.44	Mandibles narrow with apical tooth long to slightly elongated, acute-rounded and blunt apex. Short, rounded subapical tooth of mandible with blunt masticatory margin to absence of denticles. Basal margin tuncate-rounded with obtuse basal angle.

Table 5: Percentage of variance and overall shape variation in the right mandible as explained by each of the significant principal components of the three species of *Odontomachus.*

RIGHT MANDIBLE						
PC	% Variance	*Odontomachus bauri*	% Variance	*Odontomachus infandus*	% Variance	*Odontomachus simillimus*
1	57.55	Elongated, narrow – wide acute rounded apex of the apical tooth. Very short, truncated and blunt subapical tooth of mandible and blunt to absence of denticles masticatory margin. Basal margin emarginate with acute basal angle.	59.53	Mandibles long, with long rounded apical tooth and shorter subapical tooth with acute-emarginate 1st and 2nd teeth in the masticatory margin to mandibles with slightly longer apical tooth and significant shorter subapical tooth with blunt masticatory margin. Basal margin emarginate with obtuse basal angle.	61.39	Mandibles narrow with apical tooth slightly elongated, wide acute-rounded and blunt apex. Short, rounded-emarginate subapical tooth with blunt masticatory margin to absence of denticles. Basal margin rounded-emarginate with obtuse basal angle.
2	26.80	Elongated, narrow – wide acute rounded apex of the apical tooth. Very short, truncated and blunt to absence of subapical tooth of mandible and blunt to absence of denticles masticatory margin. Basal	14.57	Mandibles long, with longer rounded apical tooth and shorter subapical tooth with blunt and absence of dentition in the masticatory margin to mandibles with short apical and subapical teeth with blunt first two dentition in the	21.13	Mandibles narrow with apical tooth slightly elongated, wide-acute and blunt apex. Short, rounded-emarginate subapical tooth with blunt masticatory margin to absence of denticles. Basal

		margin emarginate with wide-narrowly acute basal angle.		masticatory margin. Basal margin emarginate with obtuse basal angle.		margin rounded with obtuse basal angle.
3	3.56	Elongated, acute rounded apex of the apical tooth. Very short, truncated and blunt to absence of subapical tooth of mandible and blunt to absence of denticles masticatory margin. Basal margin emarginate with obtuse – narrowly acute basal angle.	10.92	Mandibles long, with long rounded apical tooth and short subapical tooth with blunt to absence of dentition in the masticatory margin Basal margin emarginate with obtuse basal angle.	5.13	Mandibles narrow with apical tooth slightly elongated, wide acute-rounded and blunt apex. Short, rounded subapical tooth with blunt masticatory margin to absence of denticles. Basal margin rounded-emarginate with obtuse basal angle.
4	2.84	Elongated, acute rounded apex of the apical tooth. Very short, truncated and blunt to absence of subapical tooth of mandible and blunt to absence of denticles masticatory margin. Basal margin emarginate with acute basal angle.	6.39	Mandibles long, with long rounded apical tooth and short, wider subapical tooth with blunt rounded-acute first two dentition to absence of dentition in the masticatory margin Basal margin emarginate with obtuse basal angle.	3.08	Mandibles narrow with apical tooth slightly elongated, wide acute - rounded and blunt apex. Short, rounded-emarginate subapical tooth with blunt masticatory margin to absence of denticles. Basal margin rounded with obtuse basal angle.
5	2.07	Elongated, acute rounded apex of the apical tooth. Very short, truncated and blunt to absence of subapical tooth of mandible and blunt to absence of denticles masticatory margin. Basal margin emarginate with acute basal angle.	1.91	Mandibles long, with long acute-rounded apical tooth and short, wider subapical tooth with blunt to absence of dentition in the masticatory margin Basal margin emarginate with obtuse basal angle.	2.07	Mandibles narrow with apical tooth slightly elongated, wide acute - rounded and blunt apex. Short, rounded subapical tooth with blunt masticatory margin to absence of denticles. Basal margin truncate-rounded with obtuse basal angle.
6	1.56	Elongated, acute rounded apex of the apical tooth. Very short, truncated and blunt to absence of subapical tooth of mandible and blunt to absence of denticles masticatory margin. Basal margin emarginate with obtuse – narrowly acute basal angle.	1.29	Mandibles long, with long rounded apical tooth and short, wider subapical tooth with blunt to absence of dentition in the masticatory margin Basal margin emarginate with obtuse basal angle.	1.57	Mandibles narrow with apical tooth slightly elongated, wide acute - rounded and blunt apex. Short, rounded-emarginate subapical tooth with blunt masticatory margin to absence of denticles. Basal margin rounded-truncate with obtuse basal angle.

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