A Taxonomic Morphometric Analyses between Extinct Dominican Amber Fossilized Formicidae from the Miocene and Extant Dominican Formicidae

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Abstract — **This study analyzes Dominican fossil-ants from the Miocene epoch (20 MYA). The objective is to infer ecosystem changes from the evolutionary change over 20 million years by comparing Miocene Formicidae fossils to modern Holocene specimens. Morphometric data, consisting of body measurements, were gathered from fossil ants and compared to those of modern ants. The comparison showed an overall decrease of Formicidae diversity. There are also some traits that collectively exhibited evolution over time. Many traits, however, remained static. The evolutionary changes observed indicate some driving environmental change which exerted selective pressures—forcing adaptation. The fact that many phenotypes remained static suggests that traits remain favorable and that environmental changes over 20 million years were not dramatic.**

I. INTRODUCTION

Perhaps one of the most disregarded yet fascinating ecological impacts and evolutionary stories involves the humble Formicidae, or ant. Ants are architects of the ecosystem, affecting both species diversity and density around them.[1] All Formicidae display eusocial tendencies including altruistic behaviors. Eusocial tendencies, a notorious non-morphological synapomorphy of Formicidae, has led to their expansion and dominance over the world ecosystems, including every highly populated continent today.[2] Ants first appeared in the fossil record about 100 million years ago during the Cretaceous.[3] During the Eocene around 50 million years ago, the number of Formicidae fossils discovered dating back to this era rose significantly, suggesting the start of ant dominance.[3]

Formicidae fossils have been found worldwide, and significant amounts of these fossils derive from the Caribbean island of Hispaniola (Barden 2016). Hispaniola is home to a tropical environment making the island a prime location for biological diversity and evolution. Furthermore, Hispaniola splitting from the Greater Antilles allows for geographic isolation leading to allopatric speciation. The island also allows for limited genetic drift, as all alleles present on the island will not deviate. Amber, fossilized tree resin, is abundant in Hispaniola. This resin provides near immaculate preservation of morphological details on ants, essentially providing a window into the Miocene (Sherratt et al. 2015). This study looks at previously described Formicidae fossils from Hispaniola dating back to the Miocene. Morphometric analyses consisted mainly of incorporating head length, head width, eye length, eye width, mandible length, procoxa length, Weber's length (length of mesosoma), and the cephalic index (ratio of head length to head width. Analyses were conducted on all extant discoveries of the genera present today on Hispaniola as well as during the early Miocene; a further restriction of data to only Hispaniolan fossils was also imposed.

Fossil ants and extant ants have not been used in studies together. Moreover, polymorphism in fossil Formicidae, temporal information, and geographic and ecosystem distribution depend on fossil data to determine. While there still are gaps in the fossil record, with the discovery of numerous amber fossilized Formicidae specimens in Hispaniola amber deposits, further studies to advance the evolutionary understanding of these organisms are possible. Therefore, it is asked: Is there a significant difference between phenotypes of ancient Dominican Formicidae genera and extant genera? This study aims to infer evolutionary trends of Formicidae that have resided on Hispaniola. To sum, because evolution is responsible for the diversity of life on earth, empirical studies allow observation of evolution, and ants having a rich fossil record to study, ants were chosen as a paradigm of evolution. This aims to observe evolutionary trends over time through ants and amber.

II. METHODS

All extant species of Formicidae known on Hispaniola were compiled and sorted by genera. There were 401 extant Formicidae species found. Compiling a list of all fossilized Formicidae known followed, and was also sorted by genera. There were 96 specimens in 66 different species found, including private specimens from the Barden collection at NJIT. Both lists of genera were analyzed and an exhaustive list incorporating all Formicidae genera from the Miocene that survive today. There were 21 genera total surviving today from the Miocene.

After compiling a comprehensive list of Formicidae genera present today and in the Miocene, measurements were taken of all specimens with available measurements. These measurements included head length, head width, mandible length, eye length, eye width, procoxa length, and Weber's Length (mesonomal). Total length was not measured due to the expandability of the gaster, the last segment of the ant. Therefore, gaster lengths, as well as total length, were excluded.

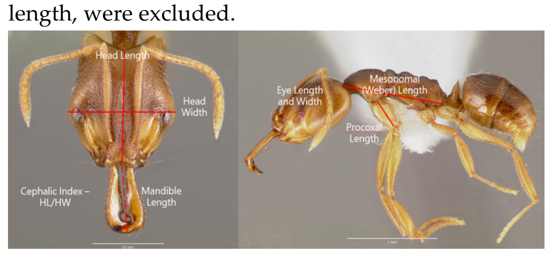

Figure 2: Static phenotypical measurements and indices of Formicidae taken include the head length, head width, mandible length, eye length, eye width, procoxal length, mesonomal (Weber's) length. The only index analyzed was cephalic index. Measurements in millimeters. Images adapted from AntWeb.

Statistic approaches were considered before analysis. The final statistical output included principal component analyses between all extant and extinct Formicidae on Hispaniola to determine morphospace occupied. A paired t-test for each morphometric measurement between all genera, giving an indication of the ecological niche in which the Formicidae resides as well as evolutionary changes in head shape in each genera.

III. RESULTS AND DISCUSSION

Evolution was shown not only occurring within a genus but on the island community of Formicidae as a collective. A paired 2-tail t-test was ran between all phenotypical features. Phenotypical adaptations were seen within the island Formicidae community as a collective. There was a significant difference between extinct and extant head lengths, head widths, Weber's (mesonomal) lengths, and cephalic indices of extinct and extant ants. The data suggested head sizes increasing over time. This bigger ant trend is also seen with Weber's length, which showed adaptation to become longer and larger. However, a limitation of this argument stems from the sampling error. It cannot be assumed that all extinct fossils have been accounted for, therefore the increase in head size is only a proposal. This applies to Weber's length as well. While the data indicate that the mesonomal length evolved to become larger, there could still be undescribed ants, which could deviate the mean of the extinct ants in an upwards direction.

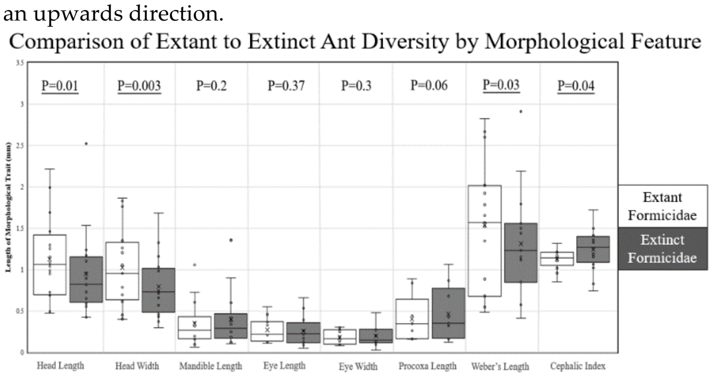

Figure 3: Each genus' morphology was averaged to create 1 data point. This is a comparison between averages of all genera within 1 measurement between the extant and extinct ants. P values from Paired 2-tail t-tests displayed.

The only collective shift that is assumed to be completely verified regards the cephalic index. The cephalic index of Miocene ants showed higher diversity and spread a larger range than modern Holocene ants. There was a significant difference of p=0.04 with extinct ants having a larger cephalic index than modern ants—indicating their heads were generally more elongated, on average across genera. Furthermore, because the morphospace occupation of extinct ants transcends that of extant ants, it can be concluded the diversity of head shape has decreased. The current interquartile range of cephalic index is extremely narrow, and centering just over 1. This suggests that head sizes have evolved from many diverse niches and converged on one generally favorable head shape that is only slightly elongated vertically, but mainly circular or square. This indicates the presence of a selective factor that induced this evolutionary change.

The multivariate statistical technique Principal Component Analyses (PCA) were ran on each genus. The variables included all measurements excluding the cephalic index. Presented to the left in Figure 4 is the principal component analysis for all ants discovered from the Miocene and modern ants on Hispaniola. Because the extant Formicidae plot occupies less morphospace than the extinct Formicidae, which extends beyond the morphospace of the extant population, it can be concluded that variation has decreased over the 20 million years. This indicates an environmental shift or selective pressure that caused natural selection to favor ants of a specific phenotype within the extant ants. Many extreme ants, indicated by the outermost points on the extinct morphospace plot, have either evolved to converge onto extant phenotypes or have become entirely extinct. This indicates evolution occurring on Hispaniola over the 20 million years since the Miocene, driven by selective pressures.

PCA plots also supported this shift in diversity. The principal component analysis ran between select genera including *Anochetus, Odontomachus, Platythyrea, Pheidole,* and *Pseudomyrmex* showed extant and extinct ants occupying differing morphospace. These five genera, selected from 21, showed almost no overlap in morphospace. This indicates that the ancient Miocene environment on Hispaniola were conducive towards certain morphotypes. However, as the environment slightly shifted, many morphotypes were selected resulting in the success and radiation of Formicidae belonging to other niches

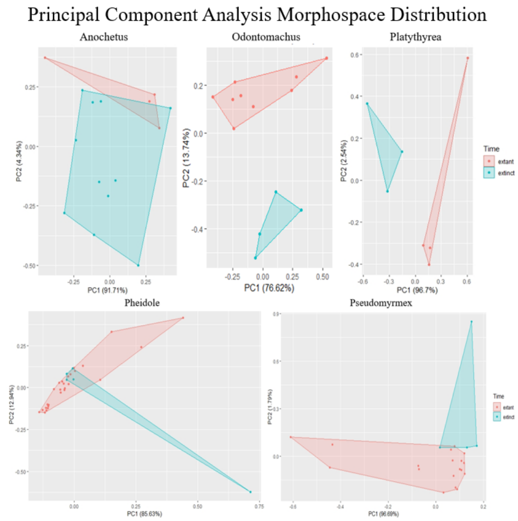

Figure 4: Principal component analysis between select Formicidae genera on Hispaniola. Red dots represent extant species while blue dots represent extinct species. Results indicate shift and reduction in Formicidae diversity over time.

The study presented here exemplifies the intricate nature of evolution, especially when studied in the microcosm of the world of Formicidae. Results indicate the reduction in diversity of overall ant morphospace on Hispaniola, especially including cephalic indices and overall head shape, perhaps due to selective pressures on the island as a whole. Furthermore, there is variation in how different genus compositions have changed over time. Evolutionary patterns from the Miocene to the Holocene could be due to the gradual cooling of the global climate. The gradual cooling may not have been favorable towards extremes along the spectrum of Formicidae phenotypes and morphology. Selective pressures are not limited to this, however. It is further hypothesized that anthropological involvement and invasion in Haiti and the Dominican Republic have contributed to the overall decrease in ant variation on Hispaniola. This principle holds true for the Earth's ecology as a whole, where humans have exacerbated the rate of evolution. It is urged that further studies not only confirm the findings of this study regarding morphometrics by acquiring more fossil and extant data and further analyzing for trends, but also delve into the potential of human involvement in the extinction of Formicidae species on Hispaniola, and the global biosphere as a whole.

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V. REFERENCES

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