

Ecological morphospace of New World ants

MICHAEL D. WEISER¹ and MICHAEL KASPARI² ¹Department of Ecology and Evolutionary Biology, University of Arizona, U.S.A. and ²Department of Zoology, University of Oklahoma, U.S.A.

Abstract. 1. Here the quantitative relationships between ecology, taxonomy, and morphology of ant workers are explored. The morphospace for worker ants taken from 112 genera and 12 subfamilies of New World ants is described.

2. Principal components analysis was used to characterise a morphospace based on 10 linear measurements of ant workers. Additionally, strongly covarying measures were removed to generate a simplified morphological space that uses three common and ecologically relevant traits: head size, eye size, and appendage length.

3. These morphological traits are then associated with diet and foraging substrate. For example, workers in predaceous genera tend to be small, with relatively small eyes and limbs; omnivores, while small, have proportionately large eyes and limbs. Ants that forage on surface substrates are larger and have proportionately larger eyes than subterranean foragers.

Key words: Diet, foraging, formicidae, morphology, principal components analysis.

Introduction

The relationship between form and function is axiomatic in biology, and is often assumed in studies of ecological interactions and community assembly (Miles & Ricklefs, 1984). Morphology, the size and shape of an organism, reflects a combination of the differences in ecology and phylogenetic history of species (Wainwright & Reilly, 1994). Body size, arguably the most important morphological variable, affects and is limited by physiology, trophic biology, and habitat (Peters, 1983). 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 & Matthews, 1992). Moreover, size and shape are often related and these correlated traits have consequences for how taxa experience their environments (Kaspari & Weiser, 1999).

For these reasons, ecologists often quantify and differentiate ecological and taxonomic groups using morphology (Wainwright & Reilly, 1994). For example, morphological measures that reflect diet (e.g. beak depth in granivorous

birds, head width in ants) have been used to infer processes limiting membership in species communities (Davidson, 1977; Grant, 1986). Additionally, each measure contains information not only in the form of the measure itself, but also about morphological and ecological covariates and phylogenetic effects (Derrickson & Ricklefs, 1988; Losos & Miles, 1994). Thus at least three related considerations are important in selecting traits for ecomorphology studies.

First, as size and shape covary to form interspecific allometries, species by morphology matrices contain considerable redundancies. Multivariate analyses such as principal components analysis (PCA) reduce the dimensionality of morphological data sets and create orthogonal linear combinations of the original data matrix. These new axes summarise information about the size, shape, and allometry of organisms (Legendre & Legendre, 1998). As a consequence, they may be useful in detecting ecomorphological pattern (Ricklefs & Miles, 1994).

Secondly, morphological traits are products of shared descent. Ecological similarity among morphologically similar species may thus represent the inheritance of both features from a recent common ancestor. An understanding of the phylogenetic structure of the morphological dataset provides an alternative to adaptive hypotheses for ecomorphological patterns (Losos & Miles, 1994).

Correspondence: Michael D. Weiser, Department of Ecology and Evolutionary Biology, University of Arizona, 1041 East Lowell Street, Tucson, AZ 85721, U.S.A. E-mail: mweiser@email.arizona.edu

Finally, the relationship between morphology and ecological performance is a basic assumption of community studies that use morphology as proxy for ecology. Tests of this assumption, *a priori*, strengthen inferences that come from these analyses (Miles & Ricklefs, 1984; Juliano & Lawton, 1990, 1994).

Ant ecology and morphology

Ants (Hymenoptera, Formicidae) are an interesting group for the study of morphology. Ants, like all social Hymenoptera and termites, are super-organisms (Wilson, 1971) with gynes (= 'queens') that typically perform the reproductive function for a larger number of non-reproductive neuters (= 'workers'). The morphology of an individual ant colony is thus the distribution of its workers size and shape. As workers perform the nursing, foraging, defence, nest construction, etc. for the colony the distribution of worker morphology is analogous to the morphology of appendages of non-social organisms.

Ants are conspicuous and important parts of virtually all terrestrial ecosystems (Hölldobler & Wilson, 1990; Andersen, 1991; Kaspari *et al.*, 2003). Toward understanding the function of ant communities, ecologists have often used single linear measures of size (Eastlake Chew & Chew, 1980; Fellers, 1987; Cushman *et al.*, 1993; Byrne, 1994). Head width, in particular, is often used as a measure of feeding mode and overall size as it contains information about covariates such as mandible size, cephalic musculature, and mandibular glands (Davidson, 1977; Wilson, 1978; Bernstein, 1979; Morton & Davidson, 1988; Kaspari, 1993; Byrne, 1994; Johnson, 2000). However, many morphological features that likely affect ecological performance – such as head width and leg length – covary allometrically both within species (Feener *et al.*, 1988; Diniz-Filho *et al.*, 1994), and between species and other higher taxa (Kaspari & Weiser, 1999). The goal of this work is to use current information on ant genera to build

working hypotheses of these relationships that will be useful as new natural history and phylogenetic information becomes available.

Methods

The basic aim was to measure at least one representative species from every New World ant genus, selected from the pool available in the authors' collections and the Museum of Comparative Zoology at Harvard. Genera were assigned to tribe, subfamily, and subfamily groups following Bolton (2003) and based on the growing consensus of subfamily trees (Hölldobler & Wilson, 1990; Ward, 1990; Baroni Urbani *et al.*, 1992; Ward, 1994; Grimaldi & Agosti, 2000). Family group, familial, tribal, and generic taxonomy generally follow Bolton (2003) with the exception of *Oligomyrmex* = *Carebara* (Fernández, 2004). Genera examined are listed in the Appendix.

Up to five individuals/species from a single locality/date were measured (mean = 4.4 individuals per species). For dimorphic genera (e.g. *Pheidole*, *Carebara*, *Cephalotes*, *Camponotus*) only the minor worker caste was measured. For polymorphic genera (e.g. *Eciton*, *Labidus*, *Atta*) the media caste was measured.

Ten linear traits used by ant ecologists and taxonomists were included: two measures of head size, four measures of head appendages, two of thorax size, and two of leg length (Table 1). Structures used to define higher-level (subfamily or tribe) taxonomy (e.g. post-petiole, sting) were not measured. All measures were taken using an Olympus® SZH microscope with an ocular micrometer with resolution of 0.0076 mm. Original measures are available from the first author.

Measurements

Eye size. Eye measures are frequently used in ant taxonomy. To measure the presence of eyes, and the

Table 1. Descriptive statistics for the 10 measures of ant morphology from 112 New World ant species. pWR is a gauge of variability on a log scale (see main text). Measurement repeatability is the coefficient of variation from duplicate measures of one individual from 25 species, separated by 6 months. None of the Kolmogorov–Smirnov (KS) tests found significant deviation from normality at $P < 0.05$ (KS tests on log transformed data).

	Measure	Mean (mm)	SD (mm)	Min (mm)	Max (mm)	pWR	Repeat- ability	KS $z =$
Eye size	Eye length	0.19	0.17	0.00	1.68	2.22	0.059	1.15
	Eye width	0.14	0.12	0.00	1.21	2.08	0.044	0.93
Head size	Head length	1.01	0.77	0.15	6.19	1.61	0.014	0.81
	Head width	0.90	0.67	0.25	5.68	1.35	0.015	0.71
Head appendages	Scape length	0.87	0.71	0.15	6.67	1.64	0.020	0.65
	Mandible length	0.59	0.45	0.14	4.87	1.54	0.027	0.59
Mesosoma	Pronotum width	0.62	0.46	0.15	3.61	1.38	0.012	0.61
	Alitrunk length	1.37	1.11	0.29	9.14	1.49	0.041	0.54
Leg length	Femur length	1.06	0.95	0.15	8.63	1.76	0.0205	0.56
	Tibia length	0.89	0.87	0.13	7.11	1.74	0.0448	0.66

overall size and shape of the surface area of the eyes, maximum eye length and maximum eye width perpendicular to eye length were measured. For log transformation and determination of pWR ($\log_{10}(\max/\min)$), ants without eyes (e.g. *Carebara*, *Cheliomyrmex*, *Discothyrea*, *Probolomyrmex*, *Rhopalothrix*, and undescribed species at the Museum of Comparative Zoology) were assigned the value of 0.007 mm, as the limit to our resolution was ≈ 0.0076 mm. Eyeless genera are not randomly distributed among ant subfamilies, occurring only in genera of Ectoninae, Ponerinae, and Myrmicinae sampled here (Baroni Urbani *et al.*, 1992).

Head size. Measures of head size 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.

Head appendages. Antennal scape length (collar to antennal elbow) limits the distance ahead of the ant that it receives chemosensory information. The elongation of the scape is a synapomorphy of the Formicidae (Baroni Urbani *et al.*, 1992), but scape length may show considerable variation within the family. Mandible length (from mandibular insertion to most distal point) is a simple measure of size of the mandibles.

Mesosoma. Two measures delimit the width and breadth of the mesosoma, the central axis in ants that consists of the true thorax fused to the first segment of the abdomen. These are the maximum pronotum width in dorsal view and alitrunk length from anterior edge of pronotum to posterior edge of propodeum, also known as Weber's length. Mesosoma length is a common general measure of body size, and pronotum width (along with head size) represents the cross-sectional area (Kaspari & Weiser, 1999).

Leg length. The length of an ant leg is largely taken up by the hind femur length, excluding trochanter, and hind tibia length, the stilt-like appendage connecting the femur to the tarsi. Feener *et al.* (1988) link leg length to both foraging speed and food quality in leaf-cutting and army ants.

Ant morphology is highly modified and often lacks the homologous landmarks used in vertebrate studies (Bookstein *et al.*, 1985). Therefore, some traits (e.g. mandible length) may be measured with more error than others (e.g. head length and width). To quantify measurement error, a randomised subset of one individual of 25 different species was re-measured 6 months after the initial measurements. Measurement error was estimated as the average coefficient of variation (CV) for each measure.

Ecological groups

Ant genera vary widely in diet. Several published sources were used to classify ant genera into one of four diet categories: carnivore, omnivore, granivore, and fungivore (Hölldobler & Wilson, 1990; Tobin, 1994; Brown, 2000).

Genera for which there were no data on feeding type were removed from further analyses (see Appendix). Genera were assigned to a foraging stratum (subterranean, litter, or surface) using information gleaned from the literature, personal field observations, and other sources (e.g. the ants of La Selva web-page, <http://www.evergreen.edu/ants/AntsofCostaRica.html>; J. Longino). Surface foragers are ants that almost exclusively forage above ground, on top of the litter, soil, or plant surfaces (e.g. *Pogonomyrmex*, *Atta*, *Eciton*). Litter ants forage within the interstices of leaf litter, occasionally foraging on the litter surface or underground (e.g. the Dacetini). Subterranean ants are those that live and predominantly forage under the soil surface (e.g. *Cylindromyrmex*, *Cheliomyrmex*). The distinctions between subterranean and litter and litter and surface foragers are relatively subjective. Several genera could not be assigned to a foraging stratum: *Brachymyrmex*, *Lasiophanes*, *Nothidris*, *Perissomyrmex*, *Phalacromyrmex*, undescribed genus at the Museum of Comparative Zoology (S. Cover), and *Xenomyrmex*. In both cases these generalisations are inherently imperfect, subsuming variation and emphasising the taxa of common species. Treating these data as clusters along continua of diet and exposure are first approximations necessary to generate the next generation of hypotheses using species-level data.

Statistical analyses

All analyses in this paper were performed in JMP 5.1 (SAS, 2003). The mean, standard deviation, minimum, maximum, and pWR ($= \log_{10}(M_{\max}/M_{\min})$) of each of the 10 univariate measures (Prothero, 1986) were calculated. The ratio pWR is a standardised measure of size ranges that describes the order of magnitude range for a measure. All quantitative variables were \log_{10} -transformed to approximate normality. One-sample Kolmogorov–Smirnov tests were used to test for univariate normality across species means.

To summarise the New World ant morphospace, log-transformed means of each species measure were entered into a PCA. The covariance matrix from the log-transformed means was used to determine the principal components, which allows comparison of dispersion of species in this morphospace with other analyses (Ricklefs & Miles, 1994; Nipperess & Beattie, 2004). Principal component axes that account for at least 1% of the total variation in the morphospace were retained for further analysis and discussion.

Standard least squares ANOVA was then used to evaluate the hypothesis that PCA score was independent of ecological and taxonomic group membership. If the ANOVA showed significant differences across groups, group means were compared with *post hoc* pairwise Student's *t*-tests. To test for the consistency of the ecomorphological trends within subfamilies, these analyses were also performed on the two subfamilies that showed more than one feeding type (i.e. Myrmicinae and Ponerinae).

Finally, a 'baseline' morphospace aimed at identifying the minimum number of measures that achieves the same behaviour of the full 10-character matrix was constructed. Through trial and error, measures that were redundant – that is, the descriptors showed similar angles θ in three-dimensional space (Legendre & Legendre, 1998) for the first three PC axes – were removed. This method retained a suite of three variables that preserves the (1) information of PCA morphospace (qualitative axis loadings) and (2) dispersion (magnitude of morphospace dimensionality) of the PCA based on all 10 measures.

Results

Measurements were taken from 502 ant workers from 112 genera (see Appendix). This includes most (88%) of the ≈ 127 recognised New World ant genera. These genera represent 40 of the 42 New World tribes (lacking *Lenomyrmecini* and *Leptanilloidini*), 12 of 13 extant New World subfamilies, and five of six subfamily groups (Bolton, 2003). While this work focused on New World genera, this data set encompasses $\approx 40\%$, 65% , and 62% of extant ant genera, tribes, and subfamilies respectively.

The 10 measures differed in their variability, magnitude (pWR) and repeatability (Table 1). Eye measures had the largest relative range of values – over two orders of magnitude. Measures associated with cross-sectional area (i.e. head size and pronotum width) had the smallest relative range of values (1.35–1.38 o.m. (orders of magnitude)). All

10 measures were normal after log transformation based on results of one-sample Kolmogorov–Smirnov tests (KS $z = 0.56 - 1.15$, $P > 0.05$ for all relationships, Table 1). All 10 were highly and significantly correlated. Different measures of the same structures tended to show the highest correlation coefficients (e.g. eye length vs. eye width $r^2 = 0.99$, head length vs. head width $r^2 = 0.98$, femur length vs. tibia length $r^2 = 0.99$).

The measures with the highest repeatability include pronotum width (CV = 0.012), head width (CV = 0.014), and scape length (CV = 0.02, see Table 2). The lowest repeatability was found with measures of eye size (eye length CV = 0.06 and eye width CV = 0.04) and tibia length (CV = 0.045).

Principal components analysis

The first three components of the PCA accounted for 98.3% of the variance in the morphospace (Table 2). Principal component I ('size') accounted for 76.4% of the variance; all coefficients of eigenvectors were positive (range = 0.21–0.50). PC I mostly reflected size variance, but, as the coefficients are not equal, retained some size allometry.

Principal component II (= 'negative eye size') accounted for 20.7% of the variance. It had negative coefficients of the eigenvectors for eye size (–0.49 and –0.54) and positive but relatively low coefficients for the remaining eight eigenvectors (0.20–0.28). Therefore, species with high values for PC II have small eyes relative to their body size.

Table 2. Results of principal components analyses.

	PC I 'Size'	PC II 'Negative eye size'	PC III 'Negative appendage length'
<i>All 10 variables</i>			
Eigenvalue	0.831	0.225	0.014
% Variance	76.4%	20.7%	1.3%
Cumulative % variance	76.4%	97.1%	98.3%
Eigenvectors			
Eye length	0.496	–0.539	0.066
Eye width	0.474	–0.486	–0.000
Head length	0.214	0.233	0.306
Head width	0.224	0.232	0.441
Scape length	0.277	0.208	–0.374
Mandible length	0.244	0.254	0.328
Pronotum width	0.220	0.208	0.306
Weber's length	0.243	0.261	0.081
Femur length	0.302	0.264	–0.379
Tibia length	0.315	0.277	–0.464
<i>Three variables</i>			
Eigenvalue	0.334	0.079	0.005
% Variance	79.8%	19.0%	1.2%
Cumulative % variance	79.8%	98.8%	100%
Eigenvectors			
Eye length	0.867	–0.498	0.033
Head length	0.281	0.544	0.790
Femur length	0.411	0.676	–0.612

Principal component III (= 'negative appendage length') accounted for 1.3% of the variance. It reflected the allometry of appendage length (femur length = -0.38 , tibia length = -0.46 , scape length = -0.37) with head size (head length = 0.31 and head width = 0.44), pronotum width (0.31) and mandible length (0.33). Head size, pronotum width, and perhaps mandible length are measures of the cross-sectional area of ants and all load positively on PC III. All three measures of long appendages (femur length, tibia length, scape length) have negative coefficients on this axis and therefore ants with larger values for PC III have shorter appendages relative to head size, mandible size, and pronotum width.

In summary, species with a high value for PC I are larger. Species with a high value for PC II have relatively small eyes. Species with high values for PC III are robust, with short appendages relative to their cross-sectional diameter.

Size and shape values were non-randomly distributed among ant taxa and natural history. There were no significant differences in size (PC I) across subfamily groups examined here (Fig. 1, Table 3). Myrmeciomorphs,

represented only by *Pseudomyrmex* here, had the largest eyes relative to their body sizes (i.e. lowest values of PC II, Fig. 1). Dorylomorphs, represented by the Ecitoninae and Cerapachyinae here, had the smallest relative eye sizes (or lacked eyes altogether). Genera with relatively long appendages (PC III) were more likely to be found among the dorylomorphs and formiccomorphs, with myrmeciomorphs yielding the smallest values (Fig. 1). Myrmiccomorphs and poneromorphs had intermediate relative appendage lengths.

Principal component I – size and natural history

Across the family Formicidae, the largest workers were found in the granivores and fungivores while the smallest workers were omnivores and predators (Fig. 1). This pattern was perhaps driven by the myrmiccomorph subfamily Myrmicinae, where omnivores and predators were not different from each other, but both were smaller than granivores and fungivores (Fig. 1). Poneromorph omnivores like *Paraponera* and *Ectatomma* tended to be larger than

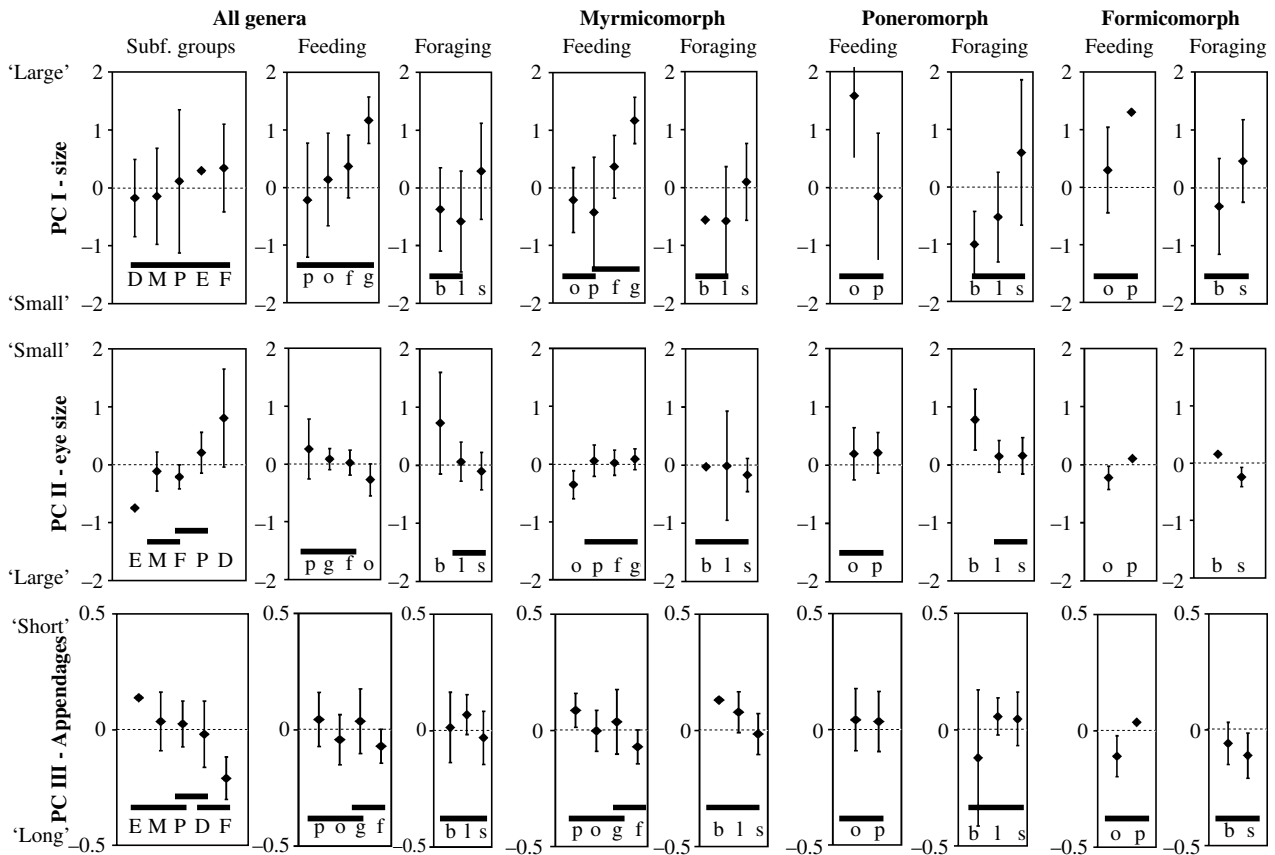


Fig. 1. Comparisons of PC I, II, and III scores to taxonomic and ecological groupings. All comparisons based on standard least-squares ANOVAs (see Table 3), with lines representing groups not different based on *post hoc* pairwise Student's *t* with $P > 0.05$. Subfamily groups: D, Dorylomorphs; M, Myrmiccomorphs; P, Poneromorphs; E, Myrmeciomorphs; F, Formiccomorphs. Feeding groups: p, predators; o, omnivores; f, fungivores; g, granivores. Foraging strata: b, subterranean; l, litter; s, surface. See Appendix for taxonomic and ecological assignments. Subf., subfamily.

Table 3. Results of ANOVAS comparing variance in principal components scores amongst taxonomic and ecological groupings.

		All genera				Myrmicomorphs				Poneromorphs				Formicomorphs			
		SS	d.f.	F	P	SS	d.f.	F	P	SS	d.f.	F	P	SS	d.f.	F	P
PC I	Whole model	4.4	11	1.3	0.258	11.3	7	2.88	0.0132	12.2	22	3.7	0.0287	2.13	20	1.30	0.3077
	Subfamily group	3.8	4	1.3	0.258	–	–	–	–	–	–	–	–	–	–	–	–
	Feeding type	4.5	4	1.6	0.181	5.7	3	2.57	0.0492	4.13	1	3.8	0.0661	0.75	1	1.37	0.2588
	Foraging type	8.2	3	3.9	0.010	3	2	2.04	0.1198	4.35	2	2.0	0.1662	1.16	1	1.06	0.3670
PC II	Whole model	12.4	11	9.07	<0.0001	2.2	7	3.7	0.0026	0.72	22	2.3	0.1153	0.44	20	5.89	0.0060
	Subfamily group	1.8	4	3.6	0.009	–	–	–	–	–	–	–	–	–	–	–	–
	Feeding type	1.5	4	3.0	0.022	1.9	3	5.6	0.0008	0.005	1	0.05	0.8244	0.13	1	5.14	0.0367
	Foraging type	1.5	3	3.9	0.011	0.1	2	0.4	0.7670	0.72	2	3.4	0.0557	0.34	1	6.74	0.0070
PC III	Whole model	0.5	11	4.9	<0.0001	0.2	7	4.7	0.0004	0.05	22	1.2	0.3547	0.03	20	1.24	0.3271
	Subfamily group	0.2	4	5.3	0.0007	–	–	–	–	–	–	–	–	–	–	–	–
	Feeding type	0.1	4	2.6	0.0379	0.09	3	3.3	0.0177	0.00	1	0.00	0.9437	0.02	1	2.87	0.1083
	Foraging type	0.03	3	1.2	0.3043	0.01	2	0.8	0.4834	0.05	2	1.7	0.2060	0.01	1	0.60	0.5624

poneromorph predators, which covered the entire size range from *Hypoponera* to *Dinoponera*.

Foraging substrate was associated with size across all species. Surface foragers were larger than litter and subterranean foragers ($F_{2,106} = 2.88$, $P = 0.0132$, Fig. 1). This pattern was consistent among two of the three subfamilies groups examined, the formicomorphs where the subterranean formicines (*Acropyga* and *Acanthomyops*) were smaller than the remaining surface taxa; and the myrmicomorphs, where litter foragers (e.g. the tribe Dacetini) were smaller than surface foragers (predominantly Pheidolini).

Principal component II – eye size and natural history

Across genera, omnivorous ants had larger eyes relative to their body size than predators, granivores, and fungivores ($F_{3,108} = 9.07$, $P < 0.0001$, Fig. 1). This pattern was consistent in both myrmicomorph and formicomorph omnivores, which had larger eyes than the other feeding types. There was no difference between poneromorphs omnivores and predators.

Litter and surface foraging taxa had relative eye sizes (i.e. PC II scores) significantly different from subterranean foragers ($F_{2,106} = 3.9$, $P = 0.011$, Fig. 1). Subterranean ants had the smallest eye sizes with several (e.g. *Cheliomyrmex*, *Probolomyrmex*) that were eyeless. Litter ants were intermediate in relative eye size and surface foragers had the largest relative eye size. Poneromorph and formicomorph taxa recapitulated the subterranean < litter = surface pattern. Myrmicomorph foragers showed no significant differences in relative eye size between foraging strata.

Principal component III – relative appendage length

Relative appendage length was more predictive of feeding type than foraging strata across the genera of the

Formicidae. Fungivores tended to have relatively long appendages, while predators and omnivores had shorter appendages relative to their size ($F_{3,108} = 2.6$, $P = 0.0379$). Granivores were not different from the other three feeding types. In contrast, PC III failed to vary with foraging strata among the genera of the family Formicidae. PC III also did not vary within the three subfamily groups examined.

In sum, 10 common ant morphometrics map onto two key aspects of ant natural history. Surface foraging omnivores, for example, tend to be larger, with larger eyes than subterranean foraging predators.

Baseline morphospace

Finally, the minimum number of measures required to reconstruct the 10-dimensional morphospace was determined (Table 2). Three sets of measures had coefficients of the eigenvectors with similar sign and magnitude for the first three principal components: eyes (eye length, eye width), size (head length, head width, mandible length, pronotum width, alitrunk length), and appendage length (scape length, femur length, tibia length). The distribution of these three descriptor sets defines the first three axes of the PCA. From these three sets, head length, eye length, and femur length were entered into a PCA using the same protocol (e.g. covariance matrix, log-transformed species means, etc.) as the 10-variable PCA above.

The resulting 'baseline' morphospace retains the overall dimensionality of the 10-variable PCA (Table 2). PC I, which explains 85% of the variance, is an overall size component with all eigenvectors positive. PC II, which explains 13.4% of the variance, had eye length loading negatively, and retains the 'negative relative eye size' relationship. The nature of PC III, which explains 1.3% of the variance, is also similar to the 10-variable PC III, with negative loading for the measure of appendage length (femur length).

Discussion

Ecological studies of morphology have in the past focused on suites of coexisting species, toward understanding the origin and maintenance of niche differences (Ricklefs & Miles, 1994). This work focuses instead on the potential morphospace available in the New World Formicidae toward understanding its taxonomic structure and ecological correlates. This is the first such study to do so. Furthermore, general patterns emerge when ant size and shape are contrasted with where it forages and what it eats.

In ants, specialised predators have evolved many times from the hypothetical large-bodied generalist ancestor (Hölldobler & Wilson, 1990), often accompanied by reduction in worker size (Haskins, 1939; Brown & Wilson, 1959; Hölldobler & Wilson, 1990). Results presented here suggest the reduction in size with obligate predation is a general pattern.

Body size is also related to the way that ants act on the world around them – larger ants move over and do not ‘recognise’ small grain irregularities that smaller ants must move through (Kaspari & Weiser, 1999). The observation that surface foraging ants are larger than litter foragers and subterranean ants is consistent with this hypothesis. However, the absence of an opposite trend in appendage size contradicts this hypothesis.

Many large-bodied, generalist predators supplement their diets with plant exudates (Hölldobler & Wilson, 1990; Brown, 2000). The largest ponerine examined here, *Paraponera clavata*, while possessing a fierce sting, is mostly vegetarian, taking few insect prey (Bennett & Breed, 1985). These results indicate a relationship between ponerine worker sizes and omnivory that may warrant further investigation. Feeding on carbohydrate-rich plant fluids has been linked to competitive dominance in arboreal ants through high-tempo activity and large colony sizes (Davidson, 1997). The subfamily groups with the highest average values for PC I (formicomorphs and Pseudomyrmicinae) all have numerous arboreal specialists (e.g. *Camponotus*, *Azteca*, and *Pseudomyrmex*).

Predatory ants have relatively smaller eyes than omnivores (Fig. 1), a pattern repeated within the myrmicomorphs and formicomorphs, but not the poneromorph subfamilies. Ants use eyes for orientation and navigation (Hölldobler, 1980) as well as detecting prey and predators. If prey specialisation leads to smaller worker size and a more cryptic, hypogaecic existence, then reduction of energetically expensive eyes may follow (Gronenberg & Hölldobler, 1999). This may be evidenced by subterranean and litter foraging ants having smaller relative eye sizes than surface foraging ants (Fig. 1).

Ecomorphological studies are labour intensive, but the 10-character morphospace can be reduced to three baseline measures – eye length, head length, and femur length – that combine repeatability, usefulness in predicting mass (Kaspari & Weiser, 1999) and frequency of use in current ant studies. While these three measures may ignore potentially important variation within genera and species, they

are recommended for ecomorphological studies across ant assemblages.

This analysis should be considered a first step towards understanding the ecomorphology of ants. We see three paths for further research. Quantitative natural history (e.g. per cent of diet from predation, herbivory, etc.) will foster more finely tuned functional comparisons across ecological continua (Tschinkel, 1991). Community-level morphometrics of co-occurring species will strengthen inferences about the relationships between morphology and ecology. Finally, genus-level phylogenies will allow exploration of the evolutionary of ant functional ecomorphology.

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Appendix 1. Taxonomic and ecological assignments used in this analysis.

Subfamily Group	Subfamily	Tribe	Genus	Feeding Type	Foraging Type	
Dorylomorph	Cerapachyinae	Acanthostichini	<i>Acanthostichus</i>	Predator	Subterranean	
		Cerapachyini	<i>Cerapachys</i>	Predator	Litter	
		Cylindromyrmecini	<i>Cylindromyrmex</i>	Predator	Subterranean	
			<i>Sphinctomyrmex</i>	Predator	Subterranean	
	Ecitoninae	Cheliomyrmecini	<i>Cheliomyrmex</i>	Predator	Subterranean	
			<i>Eciton</i>	Predator	Surface	
		Ecitonini	<i>Labidus</i>	Predator	Surface	
			<i>Nivamyrmex</i>	Predator	Surface	
			<i>Nomamyrmex</i>	Predator	Subterranean	
			<i>Azteca</i>	Omnivore	Surface	
Dolichoderinae	Dolichoderini	<i>Dolichoderus</i>	Omnivore	Surface		
		<i>Dorymyrmex</i>	Omnivore	Surface		
		<i>Forelius</i>	Omnivore	Surface		
		<i>Linepithema</i>	Omnivore	Surface		
		<i>Liometopum</i>	Omnivore	Surface		
		<i>Tapinoma</i>	Omnivore	Surface		
		<i>Technomyrmex</i>	Omnivore	Surface		
		Formicomorph	Camponotini	<i>Camponotus</i>	Omnivore	Surface
				<i>Formica</i>	Omnivore	Surface
			Formicini	<i>Polyergus</i>	Predator	Surface
<i>Gigantiops</i>	Omnivore			Surface		
Formicinae	Lasiini		<i>Acanthomyops</i>	Omnivore	Subterranean	
			<i>Acropyga</i>	Omnivore	Subterranean	
			<i>Lasiophanes</i>	Unknown	Unknown	
			<i>Lasius</i>	Omnivore	Surface	
			<i>Myrmecocystus</i>	Omnivore	Surface	
			<i>Brachymyrmex</i>	Omnivore	Unknown	
Formicomorph	Plagiolepidini	<i>Myrmelachista</i>	Unknown	Surface		

Myrmeciomorph	Pseudomyrmicinae	Paratrechina	Omnivore	Surface	
		Prenolepis	Omnivore	Surface	
		Pseudomyrmex	Omnivore	Surface	
		Tatuidris	Predator	Litter	
		Acromyrmex	Fungivore	Surface	
		Apterostigma	Fungivore	Surface	
		Atta	Fungivore	Surface	
		Cyphomyrmex	Fungivore	Litter	
		Mycetarotes	Fungivore	Surface	
		Mycetophylax	Fungivore	Surface	
Myrmicinae	Attini	Mycocepurus	Fungivore	Litter	
		Myrmicocrypta	Fungivore	Surface	
		Sericomyrmex	Fungivore	Surface	
		Trachymyrmex	Fungivore	Surface	
		Basiceiros	Predator	Surface	
		Eurhopalothrix	Predator	Litter	
		Octostruma	Predator	Litter	
		Protalaridris	Predator	Litter	
		Talaridris	Predator	Litter	
			Blepharidatta	Omnivore	Surface
	Wasmannia	Omnivore	Surface		
Myrmicomorph	Myrmicinae	Cephalotini	Omnivore	Surface	
			Procryptocerus	Omnivore	Surface
			Crematogastrini	Omnivore	Surface
			Acanthognathus	Predator	Litter
			Dacetini	Predator	Litter
			Pyramica	Predator	Litter
			Rhopalothrix	Predator	Litter
			Strumigenys	Predator	Litter
			Formicoxenini	Omnivore	Surface
			Formicoxenus	Omnivore	Surface

	<i>Harpagoxenus</i>	Omnivore	Surface
	<i>Leptothorax</i>	Omnivore	Surface
	<i>Nesomyrmex</i>	Omnivore	Surface
	<i>Ochetomyrmex</i>	Omnivore	Surface
	<i>Xenomyrmex</i>	Unknown	Unknown
Incertae sedis	<i>Adelomyrmex</i>	Unknown	Litter
	Undescribed	Unknown	Unknown
Myrmecini	<i>Myrmecina</i>	Predator	Surface
	<i>Perissomyrmex</i>	Unknown	Unknown
Myrmicini	<i>Hylomyrma</i>	Unknown	Litter
	<i>Manica</i>	Predator	Surface
	<i>Myrmica</i>	Omnivore	Surface
	<i>Pogonomyrmex</i>	Granivore	Surface
Phalacromyrmicini	<i>Phalacromyrmex</i>	Unknown	Unknown
Pheidolini	<i>Aphaenogaster</i>	Omnivore	Surface
	<i>Messor</i>	Omnivore	Surface
	<i>Pheidole</i>	Omnivore	Surface
	<i>Allomerus</i>	Unknown	Surface
	<i>Carebara</i>	Unknown	Litter
	<i>Carebarella</i>	Unknown	Litter
Solenopsidini	<i>Megalomyrmex</i>	Omnivore	Surface
	<i>Monomorium</i>	Omnivore	Surface
	<i>Nothidris</i>	Unknown	Unknown
	<i>Solenopsis</i>	Omnivore	Surface
	<i>Tranopelta</i>	Predator	Subterranean
Stegomyrmecini	<i>Stegomyrmex</i>	Predator	Litter
Stenammini	<i>Rogeria</i>	Omnivore	Surface
	<i>Stenamima</i>	Predator	Surface
	<i>Lachnomyrmex</i>	Omnivore	Litter
Myrmicomorph	<i>Tetramorium</i>	Omnivore	Surface
Poneromorph	<i>Amblyopone</i>	Predator	Litter

	<i>Prionopelta</i>	Predator	Litter
Ectatomminae	<i>Ectatomma</i>	Omnivore	Surface
	<i>Gnamptogenys</i>	Predator	Surface
Heteroponerinae	<i>Acanthoponera</i>	Unknown	Surface
	<i>Paraponera</i>	Omnivore	Surface
Paraponerinae	<i>Heteroponerini</i>	Unknown	Surface
	<i>Platythyreini</i>	Predator	Surface
Ponerinae	<i>Anochetus</i>	Predator	Litter
	<i>Belonopelta</i>	Predator	Litter
	<i>Cryptopone</i>	Predator	Subterranean
	<i>Dinoponera</i>	Predator	Surface
	<i>Hypoponera</i>	Predator	Litter
	<i>Leptogenys</i>	Predator	Surface
	<i>Odontomachus</i>	Predator	Surface
	<i>Pachycondyla</i>	Predator	Surface
	<i>Ponera</i>	Predator	Surface
	<i>Simopelta</i>	Predator	Surface
	<i>Probolomyrmecini</i>	Predator	Subterranean
	<i>Proceratiini</i>	Predator	Surface
	<i>Thaumatomyrmecini</i>	Predator	Litter
	<i>Typhlomyrmecini</i>	Predator	Surface
	<i>Proceratiinae</i>	<i>Discothyrea</i>	Predator
6 subfamily groups	13 subfamilies	41 tribes	114 genera