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RESEARCH ARTICLE

Scaling relationships in *Formica* ants with continuous worker size variation

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Abstract
Social insects exhibit highly variable body plans at multiple scales: within colonies, between conspecific colonies, and across different species. The interspecific variation in the existence and prevalence of morphologically discrete worker subcastes in social insects raises questions about the ontogeny and functional importance of alternative worker body plans. Here, we examine the allometry of four *Formica* species. *Formica* are among the most common ants in the northern hemisphere temperate zone, and species vary greatly in the degree of worker size variation. However, no *Formica* species exhibit obvious worker subcastes. By carefully measuring head width, head height, scape length, thorax length, hind femur length, and hind tibia length in 180 individuals, we confirm that *Formica* workers exhibit continuous linear scaling, meaning that they lack discrete morphological subcastes. Most measurements scale allometrically. Different colonies of the same species are generally consistent in the slope of these relationships, and we detect unexpected similarities in scaling relationships among the four *Formica* species as well. Some scaling relationships, including a proportionally shorter scape and larger head in large-bodied workers, were also previously found in fire ants. Identifying worker size and shape distributions among different species is a vital step in understanding the selection pressures shaping division of labor in insect societies.

Keywords Allometry · Body plan · Scaling · Morphology · *Formica glacialis* · *Formica neoclara* · *Formica aserva* · *Formica obscuriventris*

Introduction

Within eusocial insect colonies, individuals often exhibit dramatically different body plans. The most striking example of this variation is associated with the reproductive division of labor. Reproductive queens often differ in both size and shape from their non-reproductive worker daughters (Wheeler 1986; Trible and Kronauer 2017). Additionally, some species produce morphologically discrete worker subcastes, wherein workers from different size classes also differ in the relative scaling of their heads or appendages (Hölldobler and Wilson 1990; Miura 2005; Wills et al. 2018). For example, in the ant species *Pheidole bicarinata*, minor workers specialize in foraging and brood care, while larger soldier workers, which possess disproportionately large heads, specialize in colony defense. These *Pheidole* minor workers and soldiers are readily distinguishable based on morphology (Huang and Wheeler 2011). Morphological worker subcastes are thought to facilitate task specialization (Crosland et al. 2010), which promotes homeostasis in insect colonies (Oldroyd and Fewell 2007). However, discrete morphological worker subcastes appear to be absent from many eusocial insect species (Oster and Wilson 1978).

In social insects lacking obvious morphological worker subcastes, there are several nested levels of potential variation (Fig. 1). First, do workers exhibit variation in body size (i.e., are workers variable or uniform in size)? Second, if there is variation in body size, does the body plan remain the same between different size classes (i.e., is there isometric scaling)? Together, these two categories (uniform worker size and isometric scaling) were called 'monomorphic' by Wilson (1953). While monomorphic workers were previously thought to be common among social insect species,

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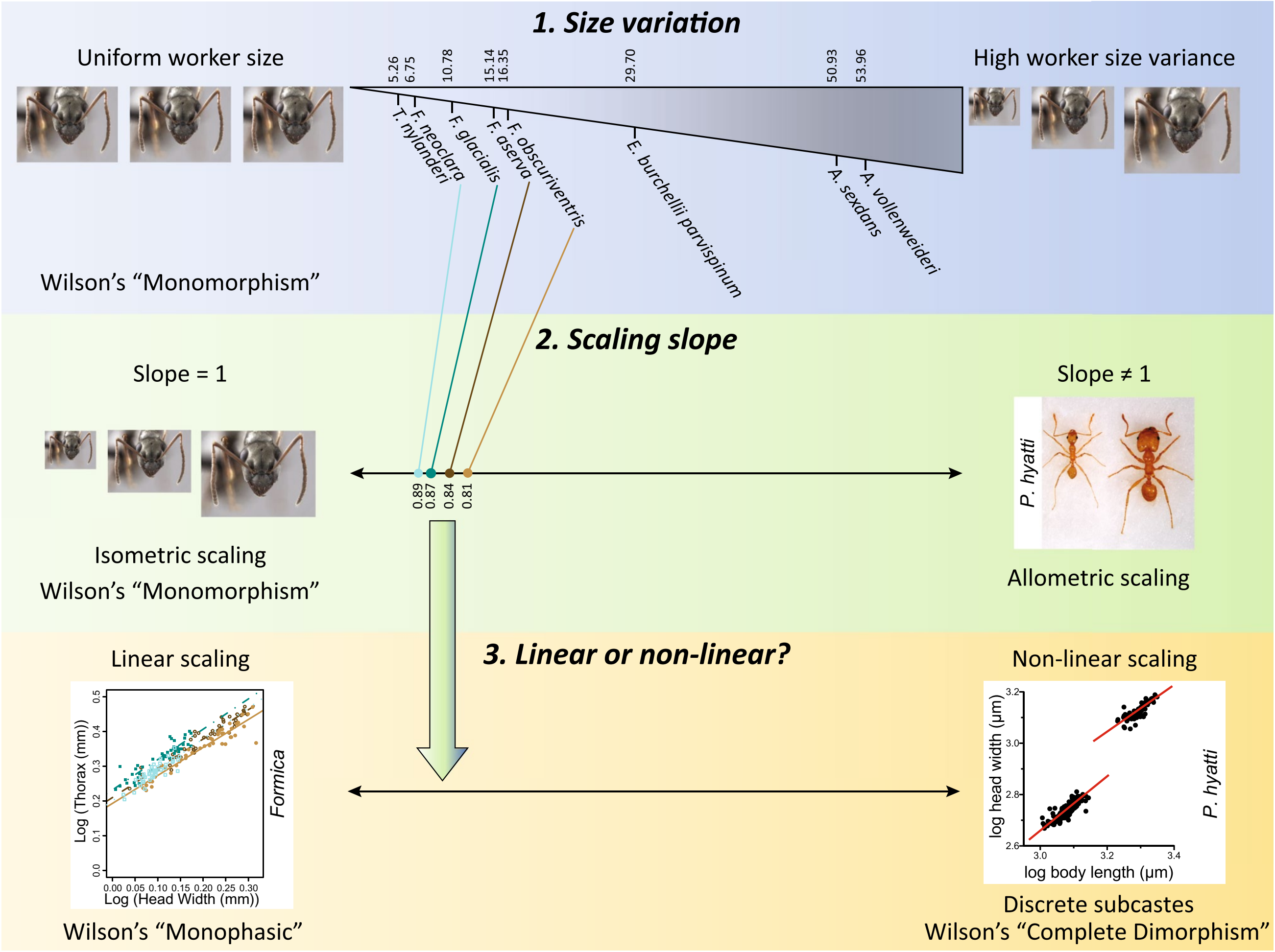

Fig. 1 General framework for understanding variance in body size and body plan in social insect workers, based on Wilson's (1953) terminology. We plotted the relative positions of our focal species along these axes, together with *Temnothorax nylanderi* (Colin et al. 2017), *Eciton burchellii parvispinum* (Baudier et al. 2015), *Atta sexdans*, and *A. vollenweideri* (Ferguson-Gow et al. 2014). In box 1, the coefficients of variation based on head width measurements for each species are plotted. In box 2, the regression slopes of the relationship between head width and thorax length are plotted for our focal species. In box 3, a plot depicting the scaling relationships between head width and thorax length in our four focal *Formica* species serves as an example of linear scaling (Wilson's 'monophasic'), while a plot depicting the scaling relationship between body length and head width in *Pheidole hyatti* serves as an example of non-linear scaling (Wilson's 'complete dimorphism'). Note that measurements are log-transformed. In the *P. hyatti* plot, estimated regression slopes are drawn in red. Figures of *Pheidole hyatti* are provided by *E. Abouheif*, based upon data published in Rajakumar et al. (2018)

careful morphometric studies of groups like stingless bees and fire ants have shown that allometric scaling, wherein body plans differ among workers of different sizes, is probably widespread (Tschinkel et al. 2003; Tschinkel 2013; Grüter et al. 2012, 2017). Third, in species with allometric scaling, researchers must distinguish between linear allometry (called 'monophasic' by Wilson 1953) and non-linear allometry (including 'diphasic', 'triphasic', or complete 'dimorphic' categories established by Wilson 1953), in which subcastes of workers may differ in scaling slope, intercept, or both. Note that the dichotomy between linear and non-linear here refers to comparisons of log-transformed measurements. Those species with non-linear allometry are considered here to have discrete morphological subcastes.

Species with linear and non-linear scaling among workers likely differ in their task allocation strategies. Such differences are most apparent in studies of task fidelity and switching. Collectively, empirical results across different species suggest that body shape plays a vital role in task efficiency and fidelity. Specifically, species exhibiting less size and shape variation potentially possess a higher degree of behavioral flexibility. In line with this pattern, dynamic task switching has been observed in *Temnothorax albipennis* (Robinson et al. 2009), a species with monomorphic workers (Dornhaus 2008). In contrast, workers in species possessing discrete subcastes are highly efficient at carrying out their typical task but rarely carry out alternative tasks. For example, submajor *Eciton burchellii* army ants transport bulky non-ant prey and are seldom observed carrying alternative loads (Powell and Franks 2005). In cases of intermediate variation among workers, social insect colonies may benefit from both efficient and behaviorally flexible workers. For example, in the size-variable stingless bee, *Tetragonisca angustula*, large workers normally specialize in and excel at nest defense, but they are capable of carrying out all of the tasks that small workers usually perform (Hammel et al. 2016). These differences are likely to be important in the face of rapid environmental change, because the colony's response to different environmental cues, such as rapid changes in food availability, is expected to depend upon the behavioral flexibility of its workers (Fisher et al. 2019).

Here, we investigate morphometrics in four *Formica* species. *Formica* exhibit extensive variation in worker size (Schwander et al. 2005; Billick and Carter 2007). Although previous studies have found that task specialization in *Formica* is associated with worker size (e.g., Bernstein 1976; Herbers 1979; Batchelor et al. 2012; Parmentier et al. 2015; Véle and Modlinger 2019; West and Purcell 2020), it is still unclear whether task specialization is also associated with differences in body plan. To this end, we measure head width, head height, scape length, thorax length, hind femur length, and hind tibia length in workers of different sizes from four species. We assess worker size variance in each species, examine the slope of the scaling relationships between head width and each of the other measures, and determine whether the scaling relationships of these measures are linear or non-linear for each species. We compare variation in scaling relationships between colonies of the same species, across the four *Formica* species that we measured, and among workers that carried out different tasks. Finally, we report scaling relationships to facilitate body size ratio inferences in future studies.

Methods

Sample collection and species background

We collected workers from three colonies each of *Formica aserva, F. glacialis, F. neoclara,* and *F. obscuriventris* in Alberta, Canada in June–August 2017. The focal species differ in their within-colony worker size variation and lifestyle. *Formica aserva* and *F. obscuriventris* are thatch mound-building species and facultative social parasites. They have relatively high within-colony worker size variation (Fig. 1). In contrast, *F. glacialis* build loose dirt mound and subterranean nests, while *F. neoclara* build subterranean nests; neither species is socially parasitic. Workers of both of the latter species are more uniform in size (Fig. 1). These four species are sympatric in many parts of Alberta. Within each species, worker body size is associated with task, with small workers generally specializing in honeydew collection from aphids and large workers specializing in nest building or protein foraging (West and Purcell 2020). We measured a total of 15 workers per colony, of which five were collected while nest building, five were collected while foraging for insect prey, and five were collected while tending aphids. This method also allowed us to identify any allometric differences that may be associated with task (external to the nest only) while also maximizing worker size variation. We measured workers that were previously collected during a mark-recapture study focused on task allocation and fidelity (West and Purcell 2020).

Morphometric measurements

Using a Leica S8AP0 microscope, we photographed ants at a magnification of 25 × with an attached Leica DMC2900 camera and measured them using the Leica Application Suite version 4.6.2. We photographed and measured 180 workers in total—15 workers from each of three colonies per species. We took six measurements: head width, head height, scape length, thorax length, hind femur length, and hind tibia length (Fig. 2). We measured the femur and tibia on one of the hind legs of each worker from joint to joint. From a lateral view, we measured the thorax from the beginning of the first thoracic segment to the petiole. From a frontal view, we measured head width as the length across the head at the widest part of the eyes and head height from the posterior-most portion of the occiput to the anterior-most portion of the clypeus. Finally, we measured the length of one of the scapes from its joint with the antennal socket to its joint with the funiculus.

Coefficient of variation

To quantify worker size variation among each of our focal *Formica* species and other ant species, we calculated coefficients of variation, defined by Ferguson-Gow et al. (2014) as:

$$\text{Coefficient of variation} = 100\left(\frac{\sigma \text{ worker head width}}{\bar{x} \text{ worker head width}}\right)$$

For each *Formica* species, we calculated coefficients of variation both at the species and colony levels. For the other species (Fig. 1), the coefficients of variation were either extracted from a previous study (*Atta sexdans* and *A. vollenweideri*: Ferguson-Gow et al. 2014) or calculated from data provided in a previous study (*Temnothorax nylanderi*: Colin et al. 2017) or available on Dryad (*Eciton burchellii parvispinum*: Baudier et al. 2015).

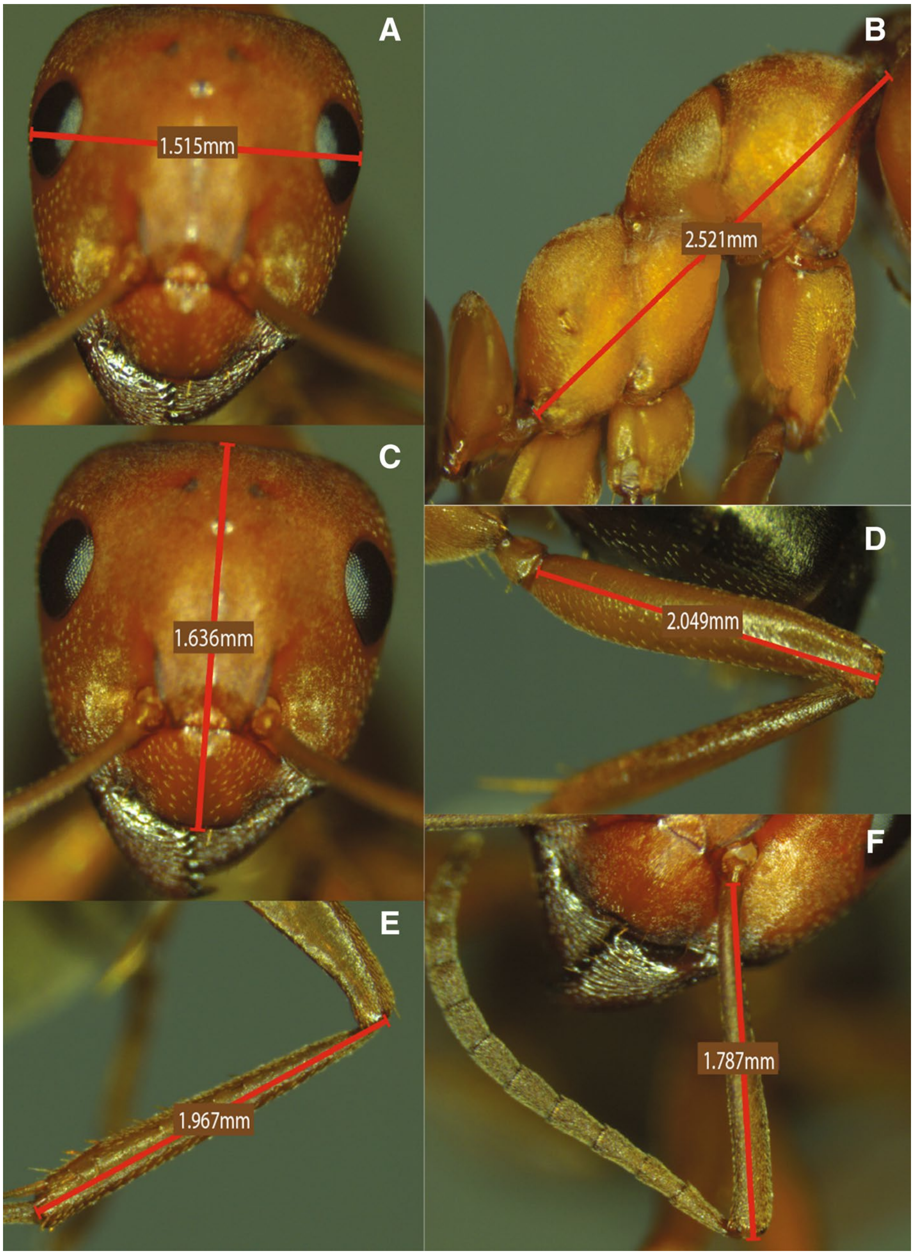

Fig. 2 Examples of head width (**a**), thorax (**b**), head height (**c**), hind femur (**d**), hind tibia (**e**), and scape (**f**) measurements

Statistical analysis

We analyzed each of the four species separately for our initial tests because we did not have an a priori expectation of trans-species scaling relationships. We log-transformed measurements and used linear models to assess associations between five morphological measurements (head height, scape length, thorax length, hind femur length, and hind tibia length) with respect to head width for each species. We also included colony and the interaction between colony and head width as fixed effects in an initial model. The interaction term between colony identity and head width was not significantly different in 19 comparisons and was marginally significant in one comparison (Table S1). In general, this means that the slopes of the scaling relationships did not differ significantly between colonies of the same species (we would expect 1/20 comparisons to be a false positive based on our alpha of 0.05; see Table S1 for colony-level analyses). As a result, we removed colony from our models and report ordinary least squares (OLS) linear regression models with each respective measurement assessed versus head width (Table 1). We used these models to calculate R^2 values, linear fit parameters, and the confidence intervals for the slope for each comparison. We checked the residuals to ensure that a linear fit was appropriate in each case.

Table 1 Overview of linear regressions for head width against five other anatomical measurements for each of the four species

	Head width			
	F. aserva	*F. obscuriventris*	*F. glacialis*	*F. neoclara*
Head height	$R^2 = 0.94$, $F_{1,43} = 653.6$, ***, $y = 0.82x + 0.06$, 95% CI 0.76–0.88	$R^2 = 0.96$, $F_{1,43} = 1099$, ***, $y = 0.89x + 0.06$, 95% CI 0.84–0.94	$R^2 = 0.94$, $F_{1,43} = 727.1$, ***, $y = 0.91x + 0.06$, 95% CI 0.84–0.98	*$R^2 = 0.91$, $F_{1,43} = 429.1$, ***, $y = 0.91x + 0.05$, 95% CI 0.82–1.00*
Scape	$R^2 = 0.85$, $F_{1,43} = 256.8$, ***, $y = 0.70x + 0.05$, 95% CI 0.61–0.79	$R^2 = 0.94$, $F_{1,43} = 731.6$, ***, $y = 0.78x + 0.003$, 95% CI 0.72–0.84	$R^2 = 0.94$, $F_{1,43} = 712.4$, ***, $y = 0.85x + 0.07$, 95% CI 0.79–0.91	$R^2 = 0.80$, $F_{1,42} = 169.6$, ***, $y = 0.82x + 0.04$, 95% CI 0.69–0.95
Thorax	$R^2 = 0.93$, $F_{1,43} = 550.6$, ***, $y = 0.84x + 0.21$, 95% CI 0.77–0.91	$R^2 = 0.90$, $F_{1,43} = 382.0$, ***, $y = 0.81x + 0.19$, 95% CI 0.73–0.89	$R^2 = 0.85$, $F_{1,43} = 241.1$, ***, $y = 0.87x + 0.23$, 95% CI 0.76–0.98	*$R^2 = 0.74$, $F_{1,43} = 124.3$, ***, $y = 0.89x + 0.20$, 95% CI 0.73–1.05*
Femur	$R^2 = 0.94$, $F_{1,43} = 656.8$, ***, $y = 0.87x + 0.10$, 95% CI 0.80–0.94	$R^2 = 0.88$, $F_{1,43} = 76.40$, ***, $y = 0.87x + 0.09$, 95% CI 0.77–0.97	$R^2 = 0.96$, $F_{1,43} = 964.8$, ***, $y = 0.92x + 0.12$, 95% CI 0.86–0.98	$R^2 = 0.93$, $F_{1,43} = 585.1$, ***, $y = 1.18x + 0.07$, 95% CI 1.08–1.28
Tibia	$R^2 = 0.89$, $F_{1,43} = 349.4$, ***, $y = 0.88x + 0.10$, 95% CI 0.79–0.97	$R^2 = 0.91$, $F_{1,43} = 446.8$, ***, $y = 0.89x + 0.10$, 95% CI 0.80–0.98	*$R^2 = 0.93$, $F_{1,43} = 546.1$, ***, $y = 1.0x + 0.11$, 95% CI 0.91–1.09*	*$R^2 = 0.81$, $F_{1,43} = 186.2$, ***, $y = 1.08x + 0.08$, 95% CI 0.92–1.24*

R^2 value, regression model F value and degrees of freedom, and the linear fit for each regression are shown. All comparisons revealed a highly significant ($p < 0.0001$ shown as ***) linear scaling relationship in each species. The 95% confidence intervals around the slope are shown for each model, and these reveal that most relationships are allometric (the slope is significantly different than 1); isometric relationships are shown in *italics*

We ran additional linear models a posteriori to examine in more detail interesting findings from our primary models. In particular, we investigated whether there were any differences among species and among workers carrying out different tasks in the slope or intercept of each scaling relationship. Acknowledging a debate among researchers studying allometric scaling, we also repeated our species-specific linear models using standardized major axis regression tests implemented in the smatr package in *R* (Warton et al. 2011). These additional analyses and results are described in more detail in the supplementary materials.

We investigated additional variation between measurements using a principal component analysis, implemented with the prcomp command in *R*. We used the get_pca command in the factoextra package to assess variable orientation and loading in this analysis (Kassambara and Mundt 2020). We performed all statistical analyses in R, version 3.5.2 (R Core Development Team).

Results

The coefficients of variation of the four *Formica* species examined in this study vary from 6.75 to 16.35 (Fig. 1). In comparison, some species with extreme morphological subcastes like *Atta vollenweideri* and *Eciton burchellii parvispinum* exhibit coefficients of variation ranging from 29.7 to 53.96 (Baudier et al. 2015; Ferguson-Gow et al. 2014). Head width is a strong predictor of each of the other body measurements in *Formica* species (R^2 values ranged from 0.74 to 0.96, Table 1, Fig. 3). The slope of most scaling relationships between head width and other measurements differs significantly from 1, indicating allometric scaling (linear fit equations shown in Table 1). In three out of four species, *F. aserva, F. obscuriventris*, and *F. glacialis*, head height and thorax length exhibit negative allometric scaling with respect to head width, meaning that their relative lengths decline as head width increases (regression $p < 0.0001$ and 95% confidence intervals for the slope do not overlap with 1 for all measurements, detailed statistical results shown in Table 1). In contrast, *F. neoclara* exhibits isometric scaling between head width and both head height and thorax length. In all four species, the relative scape length exhibits a negative allometric relationship with head width (regression $p < 0.0001$ and 95% confidence intervals for the slope do not overlap with 1 for all measurements, Table 1). In the two thatch mound building species, *F. aserva* and *F. obscuriventris*, femur and tibia lengths exhibit negative allometric scaling relationships with head width (regression $p < 0.0001$ and 95% confidence intervals for the slope do not overlap with 1 for all measurements, Table 1). Among the remaining species, *F. glacialis* exhibits negative allometric scaling and isometric scaling for comparisons of femur length

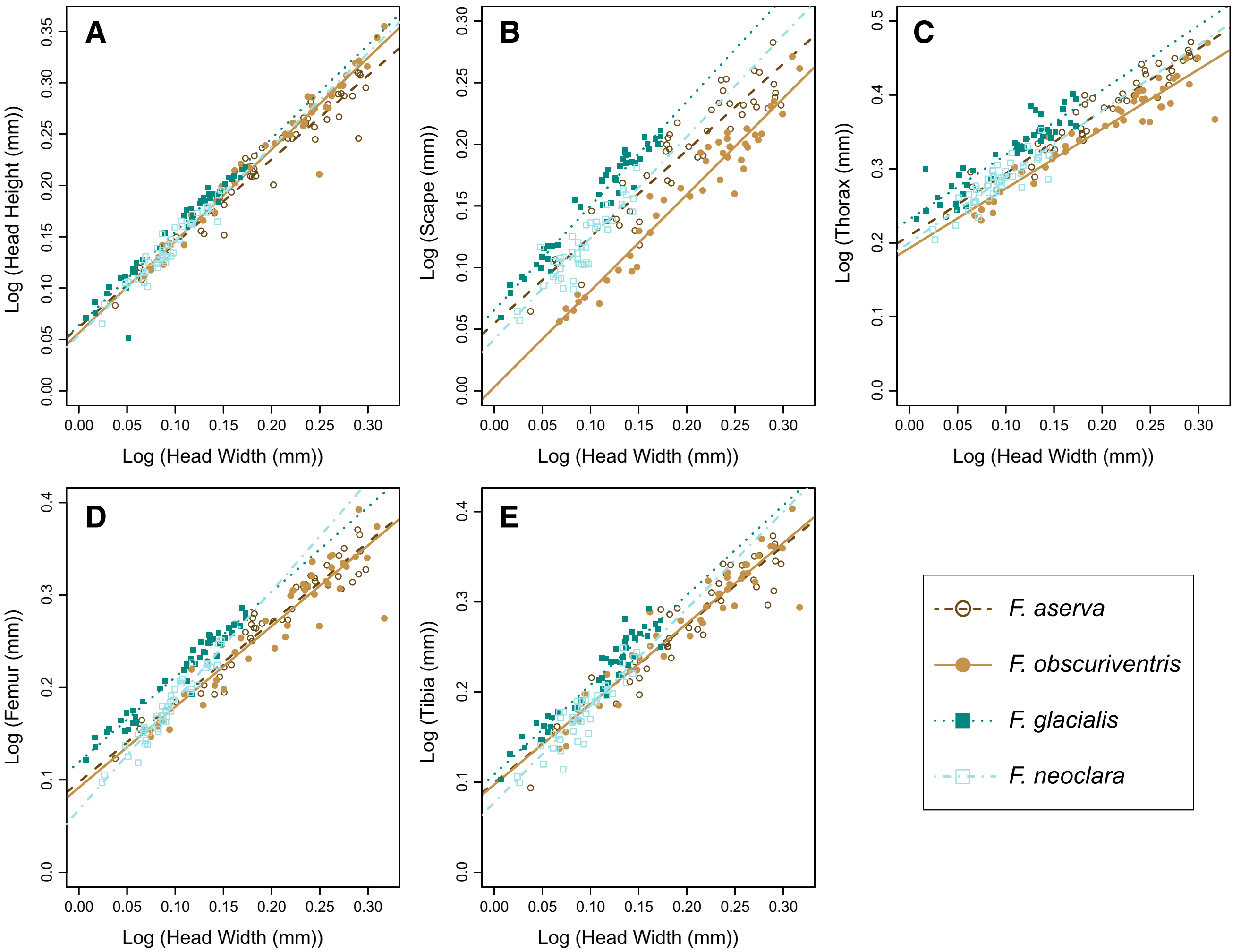

Fig. 3 Across the four focal species, all measurements were strongly associated with head width. Regressions for each of the four species (*Formica aserva,* dark brown open circles, dashed line; *F. obscuriventris,* light brown filled circles, solid line; *F. glacialis,* dark green filled squares, dotted line; and *F. neoclara,* light green open squares, dashed and dotted line) were carried out independently but plotted on the same axes for head width to head height (**a**), scape (**b**), thorax length (**c**), hind femur length (**d**), and hind tibia length (**e**) to illustrate the high degree of similarity in slope across different species

and tibia length with respect to head width, respectively (regression $p < 0.00001$ for each measurement, Table 1). Interestingly, *F. neoclara* differs from other species in leg proportions (Fig. 3d, e). The femur shows positive allometric scaling with head width, indicating that workers with wider heads have proportionally longer legs than those with narrow heads; tibia length scales isometrically with head width (regression $p < 0.0001$ for each measurement, Table 1).

Repeating these analyses using standardized major axis regression tests increases the slope values from 0.02 to 0.14 (Table S3), but minimally changes the R^2, intercept, and confidence interval values. The upward shifts in the slope of the regression lines means that the confidence intervals of seven of the 16 original allometric relationships overlapped with one, indicating that they are consistent with isometric scaling in these models (Table S3), while one of the previously isometric relationships (*F. neoclara* head width versus tibia length) shifts to be positively allometric. This comparison reveals that some of the scaling relationships identified in this study are either marginally allometric or marginally isometric, depending on the assumptions of the regression model employed. We emphasize the ordinary least squares regression results, because measurement error for head width is expected to be very small relative to variance in head width (Kilmer and Rodríguez 2016). Indeed, a second observer (MW) checked a subset of the measurements taken by ST, and repeated measures by independent observers typically differed on the order of thousandths of a millimeter.

All four species have workers with continuous size variation and no gaps or non-linear transitions in regression slope that would indicate the presence of discrete morphological subcastes (West and Purcell 2020, Figs. 3 and 4). In most cases, model residuals were evenly distributed around the mean, indicating that linear models are appropriate; occasional statistical outliers were identified and checked. In one case, an outlier resulted from a measurement error; this was corrected and the data were reanalyzed. In addition, we find only one significant difference in slope between tasks and no significant differences in intercept by task (Table S2). The slope differences between tasks for head width versus head height are slight, with the posthoc test revealing no significant differences between any task pairs in this comparison (Fig. S3).

Interestingly, we observe no significant difference in the slopes of the scaling relationships between the four measured species when comparing head width to four out of five other measurements (Table 1, 95% confidence intervals for the slope overlapped for all species). The only exception is observed in *F. neoclara* which exhibits positive allometric scaling of the femur relative to head width, compared to negative allometric scaling of the femur in *F. glacialis, F. aserva,* and *F. obscuriventris* (Fig. 3, Table 1). Including species as a factor a posteriori in models comparing all measured workers emphasized some additional differences in scaling slopes and intercepts; these differences are summarized in Table S2 and Fig. S3. The two subterranean species also tend to exhibit more isometric scaling (*F. neoclara* in three out of five comparisons, *F. glacialis* in one out of five) than the thatch mound building species with greater size variance (Table 1; SMA regression results Table S3). We note that this observation is qualitative due to the small number of species being compared in this study.

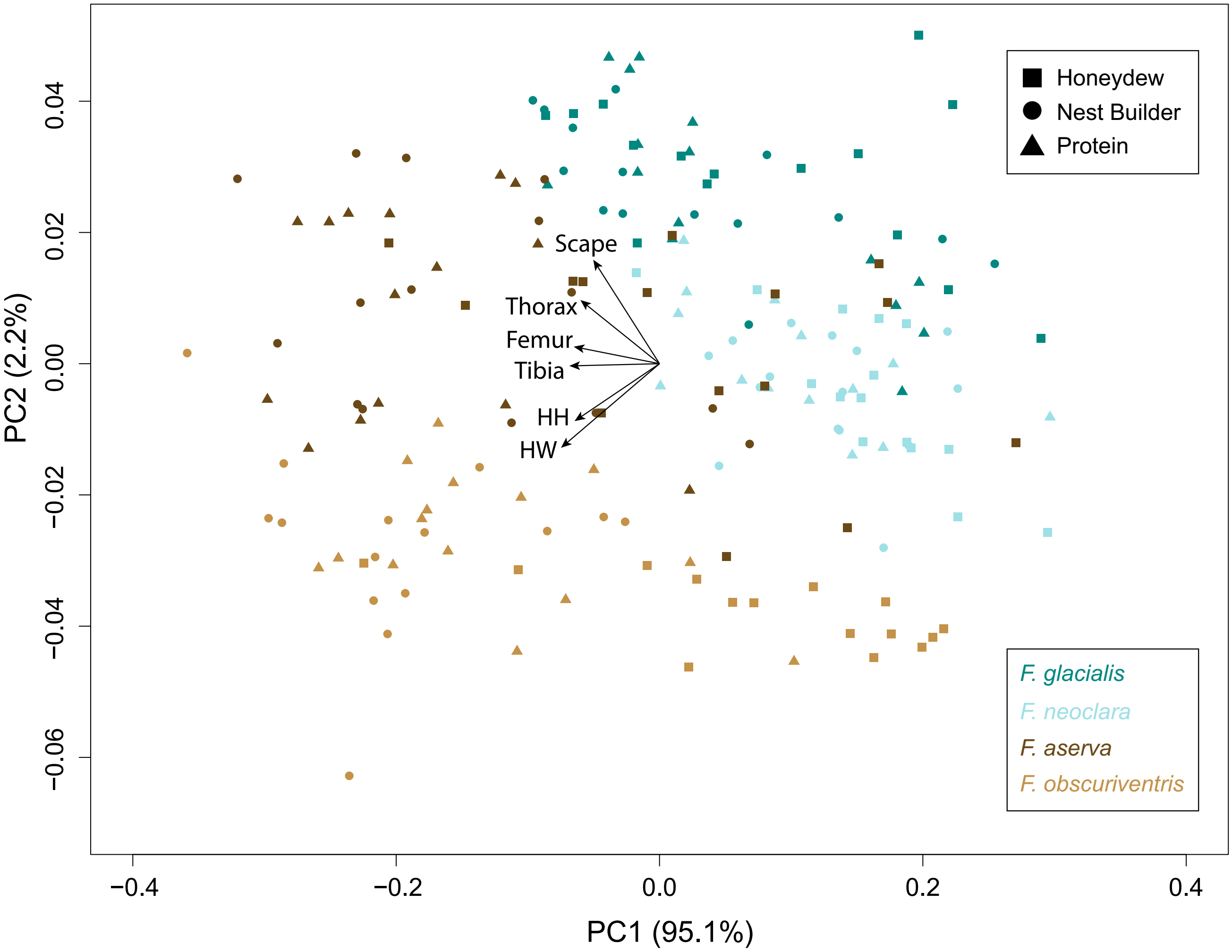

Fig. 4 PCA showing the two main axes of variation in morphometric measurements across workers of our four focal *Formica* species. PC1 reflects body size and PC2 reflects relative body shape. These axes explain 95.1% and 2.2% of morphometric variation among *Formica* workers, respectively. Vectors are drawn for scape, thorax, femur, tibia, head height (HH), and head width (HW) measurements to show the loadings of each measurement along each PC axis. Each *Formica* species is depicted in a different color, while the shape of each data point represents the task that each worker performed

We identify only one significant difference in scaling relationship between different colonies of the same species and three significant differences in y-intercept by colony (Table S1, Fig. S2). This means that body plan variation based on body size is quite consistent between colonies, even those sampled in populations separated by hundreds of kilometers (Fig. S1). The observed intercolony consistency suggests that the reported sample is sufficient to draw general conclusions about worker morphometrics in these species. Within each species, the degree of intracolonial body size variation differs across colonies, with coefficients of variation ranging from 13.19 to 18.82 (*F. obscuriventris*), 11.29 to 17.11 (*F. aserva*), 5.91 to 7.59 (*F. neoclara*), and 3.63 to 8.64 (*F. glacialis*).

A principal component analysis reveals that the majority of variance in our measurements can be attributed to size differences among species. All six morphometric measures contribute in the same orientation and with similar weightings to PC1 (weightings range from 10 to 22%; Fig. 4), which explains 95.1% of the variance. We observe some separation of species along PC2 (2.2% of the variance), where positive values indicate workers with relatively long scape lengths for their head size (Fig. 4).

Discussion

Across four *Formica* species, we observe linear scaling (usually allometric) among different morphometric measurements with respect to the head width of workers, indicating that these species lack discrete morphological subcastes. These scaling relationships are remarkably consistent among different colonies of the same species and across congeneric species exhibiting different degrees of worker size variation and different lifestyles. We discuss the implications of observing predominantly allometric, linear scaling in body plan in the context of task allocation, development, and body plan evolution and compare our results to similar studies in other social insects.

Our comparison includes two *Formica* species that build thatch mound nests and are facultatively socially parasitic (*F. aserva* and *F. obscuriventris*) and two species that are subterranean and non-parasitic (*F. glacialis* and *F. neoclara*). The former species have higher worker size variance than the latter (Fig. 1). In our initial comparison, the slopes of linear scaling relationships between head width and head height, scape, thorax length, and tibia length are not significantly different across the four species (Table 1, Fig. 3). Only the relationship between head width and femur length differs, with larger *F. neoclara* workers having longer femurs relative to their head width (positive allometry). We find additional, more subtle differences in scaling slope (marginally significant for scape) and intercept (significant differences found in all comparisons) among species with a posteriori ANCOVA models that include species as an explanatory variable (Table S2, Fig. S3). The differences in intercept among species in measurements with no significant difference in slope indicate that *F. glacialis* workers tend to have larger head heights and thorax lengths than workers of equivalent size from any of the other species, with more subtle differences among *F. aserva, F. obscuriventris*, and *F. neoclara* (Fig. S3). More generally, several of the measures that have consistent slopes across our four *Formica* species were also highlighted in a recent study of 15 *Solenopsis* species (Tschinkel 2013). In all but one *Solenopsis* species measured, the relative head width is greater in larger workers, while the relative antennal scape length is shorter. We note that our measurement and comparison methods differed from those used by Tschinkel (2013), hindering direct comparisons of slopes, but the qualitative results for these scaling relationships are consistent.

The discovery of linear allometric scaling raises questions about whether body plan differences among large and small workers are functionally relevant. West and Purcell (2020) demonstrated that *Formica* workers with different head widths consistently carry out different external tasks, including nest building, protein foraging, and honeydew collection. We find no evidence of differences in scaling relationships between workers collected carrying out each of three tasks, except for a marginally significant effect for head height (Table S2, Fig. S3). We suspect this significant relationship may be a type I error, as a posthoc test revealed no significant pairwise differences between tasks. We speculate that traits with consistent interspecific variation are more likely to have functional implications for task efficiency. For example, in line with hypotheses proposed by Tschinkel (2013) that wider heads accommodate larger and stronger jaw muscles, we suggest that larger heads may allow the larger protein foragers and nest builders to more efficiently carry large prey or nest materials. However, functional hypotheses are purely speculative at this time and require further testing for all species that exhibit linear allometric variation in worker body size.

Interestingly, *F. neoclara* workers differed from the other three species in the scaling relationship between femur length and head width (positive allometry in *F. neoclara* and negative allometry in the other species). In this species, small workers have short legs relative to the other *Formica* species, but large workers have longer legs (Fig. 3). We do not yet know whether these subtle differences among species are adaptive. One possibility is that the precise scaling relationships may serve a functional role depending on the lifestyle of each species. For example, small honeydew-collecting *F. neoclara* workers with short legs may have more efficient locomotion on small plants with narrow stems, while the other species may be more efficient at tending aphids on trees. The relatively short legs of small *F. neoclara* workers aligns with Kaspari and Weiser's (1999) size-grain hypothesis, which suggests that this body plan may be more advantageous for small organisms navigating rugose environments. On the other hand, the relatively long legs of small workers in the other three species is more consistent with their empirical findings for the ant subfamily Formicinae (the only subfamily that violated their hypothesis). Alternatively, such subtle scaling differences may be a result of different evolutionary constraints in these species and have no functional significance. Even within a taxonomic group, examining precise morphological scaling relationships in a phylogenetic context may shed light on whether or not body shape differences have adaptive value.

Linear allometric scaling could be a byproduct of developmental differences between large and small workers and, therefore, result from evolutionary constraints rather than selection. Trible and Kronauer (2017) argue that differences among worker subcastes (and queens) are determined, in part, by body size. As developing larvae grow, they propose that larvae pass different thresholds that trigger components of queen-like development. This means that larger workers should be more similar to queens. The development of alternative morphological subcastes is more generally known to rely on complex hormonal pathways and genetic networks that control how the growth of individual tissues responds to the overall growth of an individual (Abouheif and Wray 2002, reviewed in Trible and Kronauer 2017; Rajakumar et al. 2018). If this is the case in *Formica* species, it would suggest that the body plan differences between large and small workers are an outcome of differing developmental trajectories, which may or may not be shaped by natural selection. As Tschinkel (2013) points out, morphological variation among workers is partially explained by allometric growth patterns associated with size, which are likely under the control of strict allometric growth rules. If these developmental constraints were present in the common ancestor of ants, this could explain the surprising similarities between *Formica* and *Solenopsis* worker allometries (Tschinkel 2013) and the similarities across both groups in the inter-colony consistency of worker allometry (Tschinkel et al. 2003). This would not exclude the possibility that body plan differences could also have functional advantages but would have implications for how such functional advantages evolved.

On a more practical note, these results will provide a useful baseline in future studies of *Formica* ants. Researchers often use head width as a proxy for overall body size in *Formica* (e.g., Schwander et al. 2005) and in other social insects (Hahn et al. 2008; Modlmeier et al. 2013; Hagen and Dupont 2013). Since morphological measurements scale linearly with head width in these four species, this is a defensible practice in *Formica*. Future researchers can additionally use the equations describing the relationships between our five focal measurements and head width in these four species to infer body plan from single measurements. We also highlight the results of the PCA, which suggests that variation among *Formica* workers, within and across species, is mainly due to co-varying size differences across different body measurements, with only a small contribution from differences in body shape (Fig. 4).

In summary, we report scaling relationships between head width and head height, antennal scape, thorax length, hind femur length, and hind tibia length for four *Formica* species. We generate a framework through which to compare worker variation in eusocial insects (Fig. 1), and we consider the implications of body plans that vary subtly with body size (see also review by Wills et al. 2018). We urge other researchers to consider worker allometry in relation to task allocation and development in more systems that lack discrete morphological worker subcastes. Looking at the evolutionary history of body plan across social transitions (especially in bees and wasps) would provide insights into the role of selection in shaping body plan in association with task allocation. Future research should move beyond correlation to test functional differences between body plans.

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Data availability Data associated with this study are provided on Dryad, https://doi.org/10.6086/D10D53.

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