
Evolution of allometries in the worker caste of *Dorylus* army ants



Fig. 1 Workers of the epigaeic army ant *Dorylus* (*Anomma*) *molestus* climb trees in search of prey.

Abstract

The worker caste of polymorphic ant species consists of individuals of strikingly different morphologies. Most studies on polymorphic species have focused on intracolony allometries and their association with division of labour and task performance of workers of different physical subcastes. However, the factors driving the evolution of these allometries are poorly understood. Here, we analyse the importance of life-style (hypogaeic vs. intermediate vs. epigaeic) as a factor in the evolution of allometries of functionally important body traits in *Dorylus* army ants in the context of an evolutionary scenario according to which a hypogaeic life-style is the ancestral state in this group. To this end we conducted a detailed comparative analysis of the allometries of nine characters for ten species belonging to all six currently recognized subgenera and showing different life-styles. Eight of the nine traits under consideration show a clear increase in relative size from hypogaeic to intermediate to epigaeic life-style. These results strongly suggest that the ecological niche shifts necessitated adaptations in these traits. The degree of overall differentiation among species is more pronounced in larger than in smaller workers. The pattern of division of labour in the epigaeic *D. molestus* indicates that two factors that may have caused this phenomenon are new food habits and an increased need for colony defence.

Introduction

Polymorphism in the worker caste of ants has been defined as non-isometric increase in size occurring over a sufficient range of adult size variation to produce individuals of distinctly different proportions (Wilson 1953, Oster and Wilson 1978). Workers of different physical subcastes show marked but flexible task specialization (e.g. Wilson 1980, 1984, Moffett 1987, Franks et al. 2001, Hughes et al. 2003), and this is thought to enhance the efficiency of the worker caste as a whole, because workers allocate tasks to themselves for which they are morphologically specially adapted (Oster and Wilson 1978, Bourke and Franks 1995).

Physical subcastes are defined as groups of workers that underwent the same developmental programme (Wheeler 1991). The development of ant larvae is controlled by nutrition and inhibitory pheromones, but also influenced by a genetic component (Wheeler 1991, Hughes et al. 2003). The effects of environmental cues are mediated by hormones, which act at specific thresholds and cause a switch between alternative developmental pathways with associated patterns of gene expression (Evans and Wheeler 2001, Abouheif and Wray 2002). In this way the critical size at which the larva begins metamorphosis and / or the growth parameters of

tissues can be reprogrammed. Imaginal structures grow mostly only during metamorphosis once food intake has stopped, so that the allometries among different body parts reflect the outcome of competition between growing tissues for nutrients (Wheeler 1991, Nijhout and Wheeler 1996, Nijhout and Emlen 1998).

Physical subcastes of polymorphic species are usually identified based on allometries and / or the size-frequency distribution workers (Hollingsworth 1960, Raignier et al. 1974, Franks 1985, Cagniant 1991, Tschinkel 1998), but this approach has been criticised (Feener et al. 1988). As the size-frequency distribution of the standing worker population represents the sum of many or continuous brood sets modified by size-dependent mortality rates (Calabi and Porter 1989, Wheeler 1991), the use of size-frequency distributions as indicator of developmental mechanisms is problematical. Moreover multimodality is hard to demonstrate statistically. It has been shown that complex allometries can be the product of reprogramming of growth parameters (Nijhout and Wheeler 1996), but it is nevertheless hard to detect physical subcastes from smoothly curvilinear graphs. Finally, as switches between alternative developmental pathways can occur in different tissues at different times or not at all in others, interpretations concerning subcastes will depend on the choice of morphometric characters.

The allometries among body parts within ant colonies represent a form of static allometry and can often be well described by Huxley's growth function $y = b \cdot x^a$ (Huxley 1932). Artificial selection experiments and a great number of comparative studies have shown that allometries in holometabolous insects can evolve quite rapidly (Emlen and Nijhout 2000). As selection in social insects operates also at the colony level, the allometries found in ants and bumblebees differ from the allometries of solitary holometabolous insects in that they are an adaptive colony trait. Previous studies have shown that these vary between populations (Owen and Harder 1995, McArthur et al. 1997), between different families within colonies of a facultatively polygynous formicine species (Fraser et al. 2000), between young pleometrotic and haplometrotic colonies in facultatively polygynous myrmicine species (Kenne et al. 2000), with colony size (Kenne et al. 2000, Nowbahari et al. 2000) and perhaps with season (Fig. 3 in Rissing 1987).

While numerous studies have examined allometries within species, comparative analyses that may reveal which factors drive the evolution of these allometries and allow insights into the functional morphology of workers with different body proportions are generally sparse (but see Wehner 1983, 1987, Feener et al. 1988, Zollikofer 1994).

The size-grain hypothesis (Kaspari and Weiser 1999) maintains that, because the earth's surface is more rugose for smaller animals than for larger ones, the benefits of long legs

(efficient, speedy movement over a planar environment) may thus decrease with smaller body size, while their costs (larger cross-sectional area limiting access to the interstitial environment) increase. The prediction from this hypothesis that natural selection should favour proportionally shorter legs with decreasing body size has been tested and confirmed in several studies on ants (Kaspari and Weiser 1999, Espadaler and Gómez 2001, Parr et al. 2003). Examining the assumption that small ants, which have proportionally smaller legs than larger ants, are more successful in exploring environmental interstices Farji-Brener et al. (2004) found that ants that reached food baits in the most rugose experimental landscapes were 40% smaller than those that first found baits in plain landscapes. Together these results indicate that the characteristics of different spatial niches in a habitat act as selection pressures for the morphology of the ant species using these different niches. Farji-Brener et al. (2004) also suggested that colonies of polymorphic ant species could enhance their foraging success by sending out workers of different sizes to explore and forage in environments with different levels of rugosity. However, at least in some species such as polymorphic army ant species, which by definition employ obligate collective foraging, workers of different sizes work together in the same microniche. If different spatial niches in a habitat do indeed favour specific ant worker morphologies, one would expect that workers of all sizes in these species show the respective niche specific adaptations.

The army ant genus *Dorylus* represents a well-defined monophyletic group (Bolton 1990, Brady 2003) with the six currently recognized subgenera *Alaopone*, *Anomma*, *Dichtadia*, *Dorylus s.str.*, *Rhogmus*, and *Typhlopone* (Bolton 1995). The worker caste is highly polymorphic in all species studied so far (Emery 1901, Hollingsworth 1960, Raignier et al. 1974, Berghoff et al. 2002b). Gotwald (1978) proposed that the extant *Dorylus* species derive from an ancestor with a completely hypogaeic life-style and that a few species adopted an epigaeic foraging style secondarily. He based this inference on the observation that workers are eyeless and have a reduced number of maxillary and labial segments in all species regardless of life-style. The aim of the present study is to examine the importance of life-style (foraging stratum use and nesting habits) as a factor in the evolution of allometries in the *Dorylus* worker caste. While the majority of species in this group hunts and nests in the soil, members of the subgenus *Anomma* hunt in the leaf litter (e.g. *D. kohli*, *D. emeryi*, *D. opacus*, *D. gerstaeckeri*) or on the surface and in the vegetation (the typical “driver ants”, e.g. *D. wilverthi*, *D. molestus*, fig. 1). For the examination of allometries we have chosen characters whose functional value can be demonstrated or at least be inferred convincingly. They should

all be subject to diverse selection pressures in the different ecological niches and therefore likely reflect possible adaptations associated with ecological niche shifts.

Material and Methods

Samples

Specimens used for this study were collected during field work in Kenya and Uganda between March 2001 and September 2002 and stored in 70% ethanol. Additionally samples from south-east Asian representatives of the genus were provided by Stefanie Berghoff. All six currently recognized subgenera were thus covered. In some species, samples were collected from the migration trail or directly from the nest and therefore likely represent the entire size range of workers in that colony whereas for most species nests or migrations could not be found so that these samples most probably consist only of subsets of the worker caste size range. In all species workers were taken from a single colony. Intraspecific variability is low compared to interspecific variability (Chapter II). For morphometric analysis about 100 uninjured workers each were chosen from the samples so as to represent the entire size range evenly. Callow workers were excluded. Details on origin and type of sample are summarized in Table 1. Representative specimens will be deposited in the Department of Invertebrate Zoology, National Museum of Kenya, Nairobi and the Natural History Museum Berlin.

Based on own observations or information given in the literature species were categorized as exhibiting one of the following three life-styles:

Epigaeic (E) – hunting on the ground and in the vegetation; conspicuous swarm raids attracting ant birds; large, conspicuous earth nests.

Intermediate (I) – hunting in the leaf litter but not in the vegetation; swarm raids can be so conspicuous as to attract ant birds; nests have never been found (presumably as in hypogaeic species, see below).

Hypogaeic (H) – usually hunting in the soil; normally not seen in the leaf litter or on the ground except when passing through areas with hard packed soil; nests almost undetectable (see Weissflog et al. 2000, Berghoff et al. 2002a, b, 2003 for information on *D. laevigatus* and *D. cf. vishnui*).

Table 1 *Dorylus* samples used for morphometric analyses. Abbreviations: H - Hypogaecic, I - Intermediate, E – Epigaeic, N – workers from nest or migration trail, F – foraging workers.

Subgenus	Species	Life-style	Sample type	Sample origin
<i>Dichtadia</i>	<i>D. laevigatus</i>	H	N	Sitiawan, Malaysia (4°2' N 100°5' E, 0 m asl.)
<i>Rhogmus</i>	<i>D. sp.</i>	H	F	Kibale NP, Uganda (0° 34' N 30° 22' E, 1500m asl)
<i>Typhlopone</i>	<i>D. obscurior</i>	H	F	Wamba, Kenya (0° N, 37 E, 1350 m asl)
<i>Alaopone</i>	<i>D. cf. vishnui</i>	H	F	Kinabalu NP, Sabah, Malaysia (6°5' N 116°3' E)
<i>Dorylus</i>	<i>D. affinis</i>	H	N	Chogoria, Kenya (0°13'49''S, 37°37'54'' E, 1575 m asl)
<i>Anomma</i>	<i>D. emeryi</i>	I	F	Kibale NP, Uganda (0° 34' N 30° 22' E, 1500m asl)
	<i>D. kohli</i>	I	F	Mgahinga NP, Uganda (1°28' S, 29° 40' E, 2200m asl)
	<i>D. opacus</i>	I	F	Kibale NP, Uganda (0° 34' N 30° 22' E, 1500m asl)
	<i>D. wilverthi</i>	E	N	Kibale NP, Uganda (0° 34' N 30° 22' E, 1500m asl)
	<i>D. molestus</i>	E	N	Chogoria, Kenya (0°14'16'' S, 37°34'31'' E, 1842 m asl)

Division of labour

To understand why morphological differentiation is more pronounced in larger workers (see results) we additionally examined the pattern of division of labour in the epigaeically hunting *Dorylus molestus*. Workers engaged in the following activities were collected from the same colony mentioned above over a period of 2 weeks using forceps or aspirator (n given in brackets along abbreviation and more precise definitions where necessary): dropping soil particles on a slimy prey animal (144, Slime); running on foraging trail (687, Foraging); removing soil particles from foraging trench during wet weather conditions (249, Trailexc);

participating in swarm raid (777, Swarm, workers were collected from the front 20cm of the swarm); running on migration trail towards new nest (1667, Migration); defending foraging trail after disturbance (308, Traildef, workers biting into the observer's finger after blowing onto the trail with the finger placed 5 cm away from trail); carrying soil particles out of nest during dry weather conditions (299, Nexdry); transporting food items in groups (294, FGrp, all workers combined); carrying soil particles out of nest after heavy rain during previous night (273, Nexwet); transporting food item alone (136, FSing); transporting food item in group (113, Fgrp1, front runners only); standing alongside foraging trail in defensive posture (357, Defpost); cutting up earthworms (104, cutting); defending nest after disturbance (142, Nestdef, workers biting into the observer's hand after beating onto nest).

Morphometrics

All measurements were taken using a MS 5 Leica stereomicroscope fitted with an ocular micrometer. The maximum possible magnification to keep a structure within the range of the ocular micrometer was used (6.3 – 64x). We used methods recommended by Seifert (2002) to minimise measurement errors. Measurement error (ME) as assessed by repeated measurements was quantified as % ME following Bailey and Byrnes (1990) for a set of ten *D. molestus* individuals encompassing the entire size range which were scored for all characters 5 times. A one-way analysis of variance was then performed to partition variance into within- and between-individual components. The definitions, abbreviations, percent measurement errors, and presumed functional significance of the characters under consideration are as follows:

Maximum head width (HWmax, 0.27%) – maximum measurable head width. Wider heads can accommodate larger mandibular muscles and may therefore allow larger biting force (Paul 2001).

Anterior head width (HWa, 0.62%) – distance between points where mandibles touch head capsule when fully expanded with forceps. A wider anterior head width allows the mandibles to be opened wider when biting predators or prey.

Funiculus length (FL, 1.74%) – length of the left funiculus. Funiculus length should be important in trail following behaviour, especially because *Dorylus* workers are eyeless.

Longer funiculi (and scapes) will enable individuals both to follow the pheromone trail and avoid collisions at higher speeds (Couzin and Franks 2003).

Scape length (SL, 0.02%) – Maximum straight line scape length excluding the basal condyle. Functional significance see FL.

Mandible length (ML, 4.36%) – distance between apex of the left mandible to the point where it touches the head capsule when fully opened with forceps. Longer mandibles will allow more painful biting of predators and more efficient cutting of larger prey animals.

Mandible gap width (MGW, 5.15%) – distance between mandible apices when both are fully opened using forceps. A wider mandible gap allows biting of larger objects (prey or predator).

Front leg length (FLL, 1.5%) – maximum length of left hind leg from trochanter to tarsal tips in dorsal view with the leg fully extended. As prey items are carried slung beneath the body, front leg length should limit the maximum possible size of prey items. Furthermore longer legs will allow more efficient and faster locomotion.

Hind leg length (HLL, 0.87%) – maximum length of left hind leg from trochanter to tarsal tips in dorsal view with the leg fully extended. Longer legs will allow more efficient and faster locomotion and more space for other assisting workers during cooperative prey item transport, but on the other hand increase the cross-sectional area of the individual and therefore impede entering crevices (Kaspari and Weiser 1999, Espadaler and Gómez 2001). The last point should be of particular significance for species hunting in the soil.

Pronotum width (PW, 0.58%) – maximum pronotal width in dorsal view. This character was used as another size indicator (see below).

For *D. (Rhogmus)* sp. only a reduced data set (PW, HWmax, SL, FL, HLL, DM) was recorded. All measurements are in millimetres. Measurement error is generally very low, but higher for MGW and ML which reflects the fact that these measurements are difficult to make. But the differences in MGW and ML between species are sufficiently large as to allow meaningful conclusions despite lower accuracy in these measurements.

While any two linear measurements can be chosen to test for allometry and thus whether a given species complies with Wilson's definition (see above) of a polymorphic species or not, in a comparative approach one must have a general estimate of overall body size. Diniz-Filho et al. (1994) used principal component analysis in their study of polymorphism in *Camponotus rufipes* to identify which among ten morphological characters scaled most closely to isometry and could therefore be used as an indicator of overall size. However, when allometric relationships are curvilinear rather than linear, principal component analysis cannot be employed in a straightforward manner (Diniz-Filho et al. 1994). We therefore used dry mass (DM, 0.02%) as an indicator of overall size, as this should also represent a good estimate of biomass investment and therefore allow conclusions as to how colonies invest biomass in workers of different proportions. Specimens were dried at 70°C for 48h and then weighed to the nearest 0.01mg using a R 200 D balance (Sartorius GmbH, Göttingen, Germany).

For the *D. molestus* workers engaged in various tasks PW only was measured.

Statistical analysis

As the aim of the present study was a comparison of the relative sizes of certain body traits between workers of different species regardless of the specific developmental programme that generates these workers, it was not attempted to identify physical subcastes. Instead, for each trait we first established the best fit model for raw linear data from all species combined over their common size range (0.20mg – 3.67mg) as a function of $DM^{1/3}$ by stepwise multiple regression. Higher order polynomials were included if all coefficients were significantly different from zero ($p < 0.05$, Zar 1996, Fraser et al. 2000). As the goal of conducting this multiple regression analysis was to develop a model that best predicts variability in the response, and there was no interest in studying the particular relationships between the response and explanatory variables of different orders, the problems due to multicollinearity can be ignored (Graham 2003). The relative residuals (absolute residual divided by predicted value) from this common regression model were then compared using the Kruskal-Wallis Test with life style as grouping factor and the Mann-Whitney U-Test for pairwise comparisons between life-styles, as variances were heteroscedastic (Sokal and Rohlf 1995). Additionally, an identical analysis was run over the entire size range (0.05mg – 11.08mg) displayed in our samples.

Plots of raw data had initially indicated that the differences between species increased with DM both absolutely and relatively. To explore whether this is a real effect we used two tests.

For each trait the two species with the lowest and highest relative residual values over the common size range as established by the Mann-Whitney U-Test were taken to calculate the ratios between the values predicted by their respective best-fit model over their common size range. This ratio indicates the maximum differentiation between the examined species for the trait under consideration as a function of $DM^{1/3}$. In addition, for each trait the coefficient of variation (CV) was calculated for data from all species combined in 15 equally sized intervals over the common size range. It was then tested whether the CV increases with $DM^{1/3}$. A higher CV is taken to mean stronger differentiation.

In general, we did not use log-transformed data because (1) log-transformation data often did not show a normal distribution, (2) log-transformation yielded curvilinear relationships so that statistical analyses based on log-transformed data are as difficult to analyse as those based on raw (and cube-root transformed) data, and (3) $a / b \neq \log a / \log b$ so that the calculation of ratios would be confounded.

To test for size differences between *D. molestus* workers engaged in different tasks again the Kruskal-Wallis Test with task as grouping factor and additionally the Mann-Whitney U-Test for pair-wise comparisons were used (Sokal and Rohlf 1995).

Significance levels were adjusted for multiple comparisons using the Dunn-Šidák method (Sokal and Rohlf 1995).

All statistical tests were performed using STATISTICA '99 Edition (StatSoft, Inc.).

Results

In all traits under consideration life-style had a significant effect on the values of the relative residuals values (Kruskal-Wallis test, $p < 0.001$ in all cases). Except for pronotum width workers of epigaeic species always had higher values than workers of intermediate species and these showed higher values than workers of hypogaeic species (fig. 2, 3). Pronotum width values of hypogaeic workers were larger than in intermediate workers but do not differ between the latter and epigaeic workers. These results hold when the entire instead of the common size range is considered. As an illustration of the general pattern of increase in the traits Fig. 4 and 5 show bivariate plots of HLL and HWmax vs. $DM^{1/3}$. In all traits the ratios between the species with the highest residual values and the one with the lowest values increased with $DM^{1/3}$, but never in simple linear way (Fig. 6). In two traits (funiculus length and mandible gap width) the hypogaeic species with the lowest relative residual values had

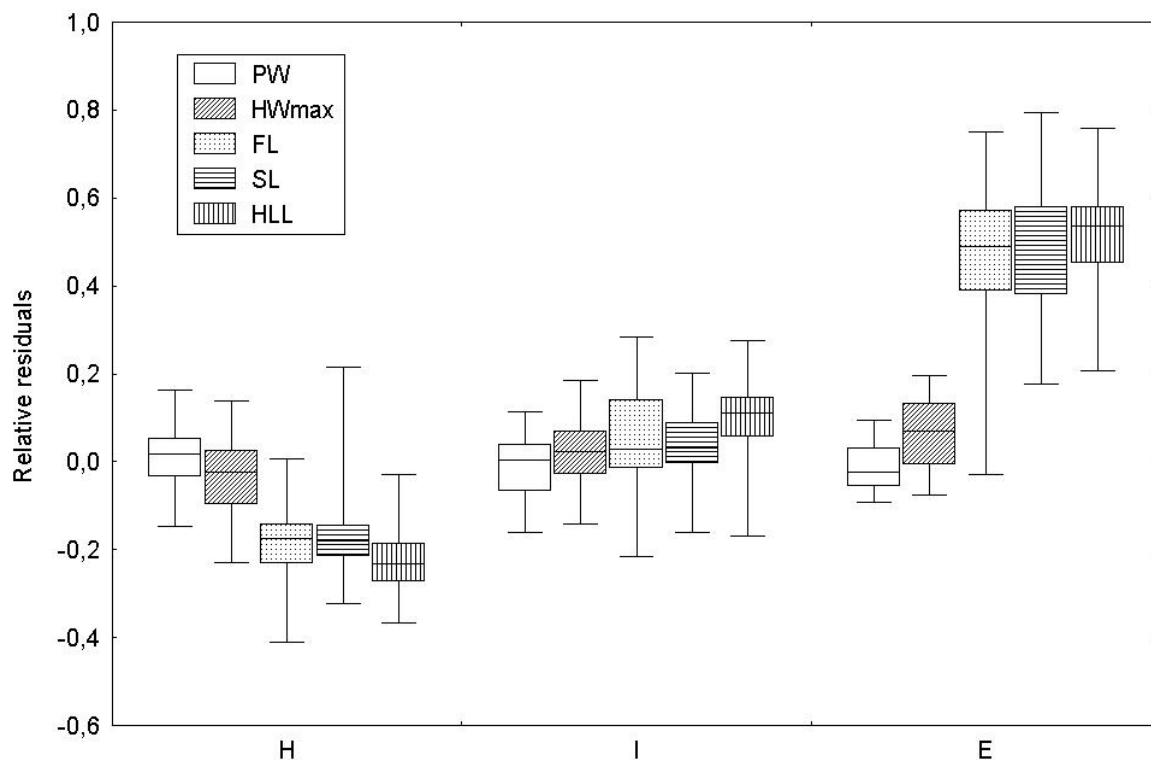


Fig. 2 Relative residuals for the traits PW, HWmax, FL, SL, HLL from common regression models over common size range for workers with different life-styles. The box encompasses the interquartile range; the internal line is the median; whiskers indicate the minimum and maximum values.

larger values for the smallest workers. CV increased significantly with $DM^{1/3}$ for all traits except SL ($r^2 = 0.219$ and $p = 0.078$ for SL, r^2 between 0.367 and 0.633, $p < 0.02$ for all others).

D. molestus workers engaged in different tasks differed significantly in size (Kruskal-Wallis test, $p < 0.0001$, Fig. 7). The groups with the highest median values are workers transporting food item singly, leading workers in food transporting groups, workers in defensive posture along foraging trail and workers defending nest and these are significantly larger than all other groups.

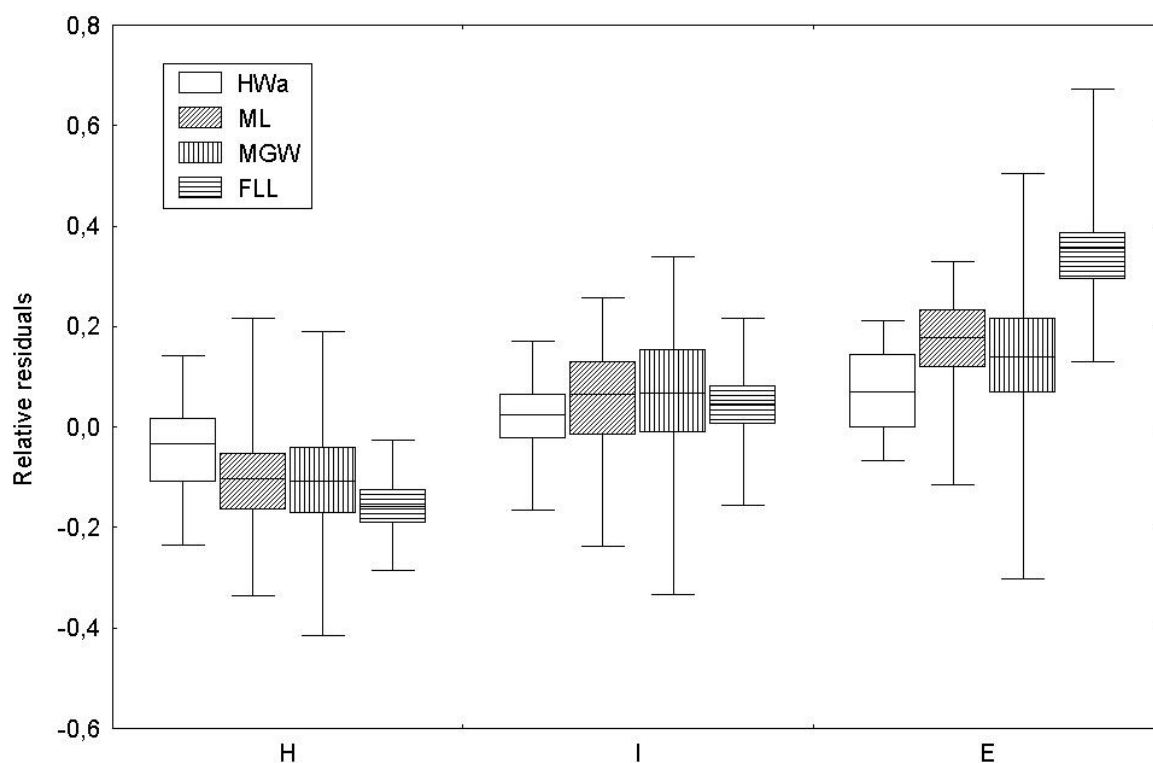


Fig. 3 Relative residuals for the traits HWa, ML, MGW, FLL from common regression models over common size range for workers with different life-styles. The box encompasses the interquartile range; the internal line is the median; whiskers indicate the minimum and maximum values.

Discussion

Dorylus species differ in their ecological niches and have often been classified into hypogaeic and epigaeic species (Gotwald 1978, Berghoff et al. 2002a), although this is an oversimplification. Species of the subgenera *Dichtadia*, *Rhogmus*, *Typhlopone*, *Alaopone* and *Dorylus s.str.* hunt and nest in the soil and are hard to find and study except for their males which fly at night and can easily be collected at light sources. As a consequence many described species in these subgenera are known from the males only (Bolton 1995). There are exceptional circumstances under which workers of these hypogaeic species appear on the surface: when foraging workers have to cross hard-packed soil (C.S. pers. observ.) or encounter unusually rich food sources (Berghoff et al. 2002a), during interspecific battles (Leroux 1979, Gotwald 1995, p. 159) and when the males emerge from the nest (Wheeler 1922). The use of ecological niches by species of the subgenus *Anomma* is more complex.

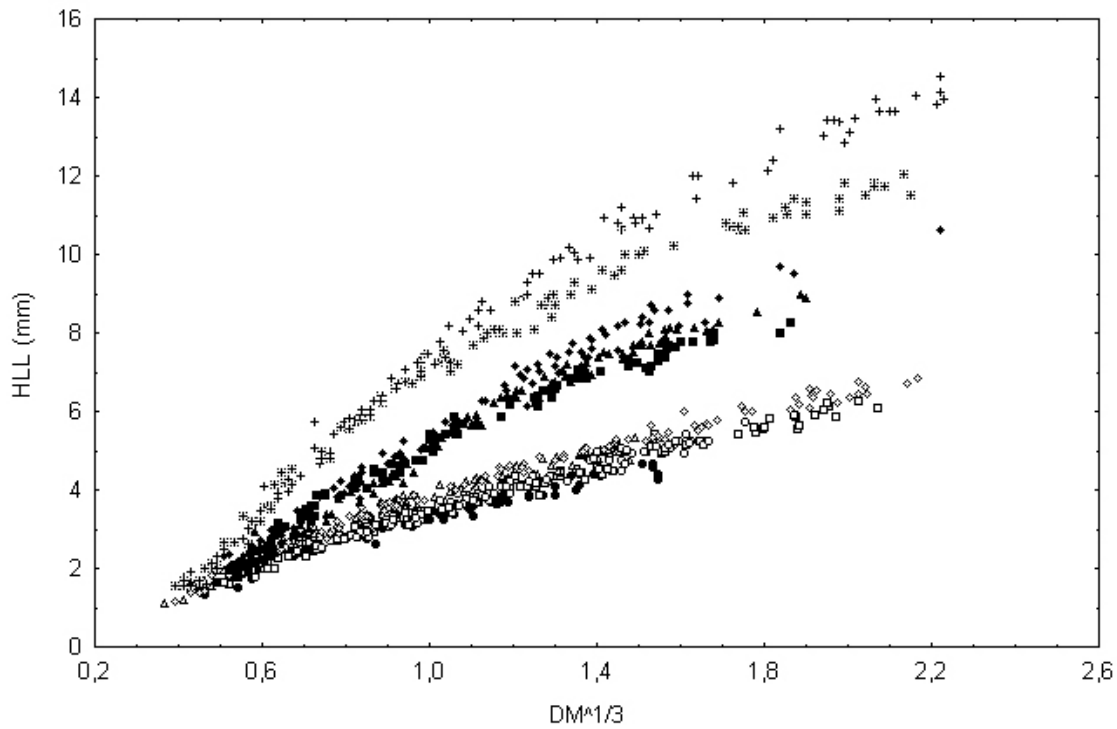


Fig. 4 HLL vs. $DM^{1/3}$ for *D. wilverthi* (+), *D. molestus* (*), *D. opacus* (♦), *D. kohli* (▲), *D. emeryi* (■), *D. (Rhogmus) sp.* (◇), *D. affinis* (Δ), *D. vishnui* (○), *D. laevigatus* (●), *D. obscurior* (□).

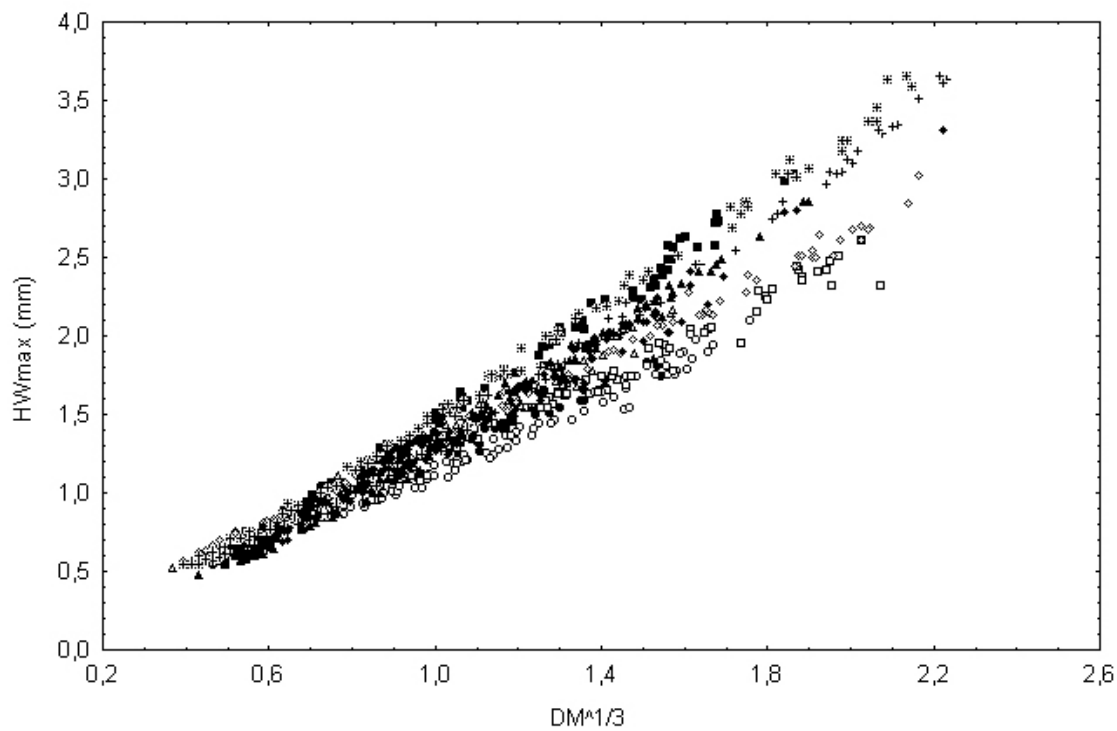


Fig. 5 HWmax vs. $DM^{1/3}$ for *D. wilverthi* (+), *D. molestus* (*), *D. opacus* (♦), *D. kohli* (▲), *D. emeryi* (■), *D. (Rhogmus) sp.* (◇), *D. affinis* (Δ), *D. vishnui* (○), *D. laevigatus* (●), *D. obscurior* (□).

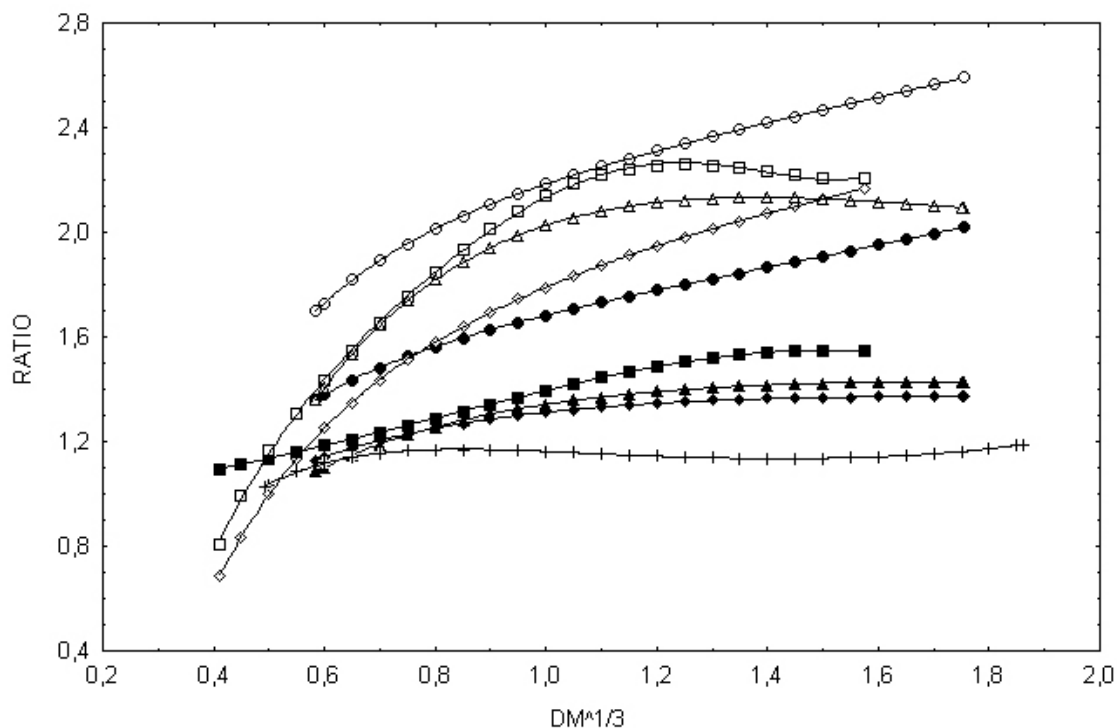


Fig. 6 Ratios between the predicted values of the species with the highest relative residuals and the predicted values of the species with the lowest relative residuals over their common size range. HLL (\circ), FLL (\bullet), MGW (\diamond), ML (\blacksquare), FL (\square), SL (\triangle), HWa (\blacktriangle), HWmax (\blacklozenge), PW (+).

While the typical “driver ants” (corresponding to our categorization “epigaeic”) conspicuously forage on the surface and climb vegetation in search of prey, several species hunt in the leaf litter stratum (“intermediate”). These differences have long been known (e.g. Wasmann 1904, Raignier and van Boven 1955, Gotwald 1974) and are even reflected in life-style specific characteristics like relative eye-size of associated myrmecophiles (Wasmann 1904).

Here we show that differences in life-style are directly correlated with differences in the allometric scaling relationships with a clear increase from hypogaeic to intermediate to epigaeic species in maximum head width, anterior head width, flagellum length, scape length, mandible length, mandible gap width, front leg length, and hind leg length. These results are in agreement with the interpretation that different spatial niches select for specific ant worker

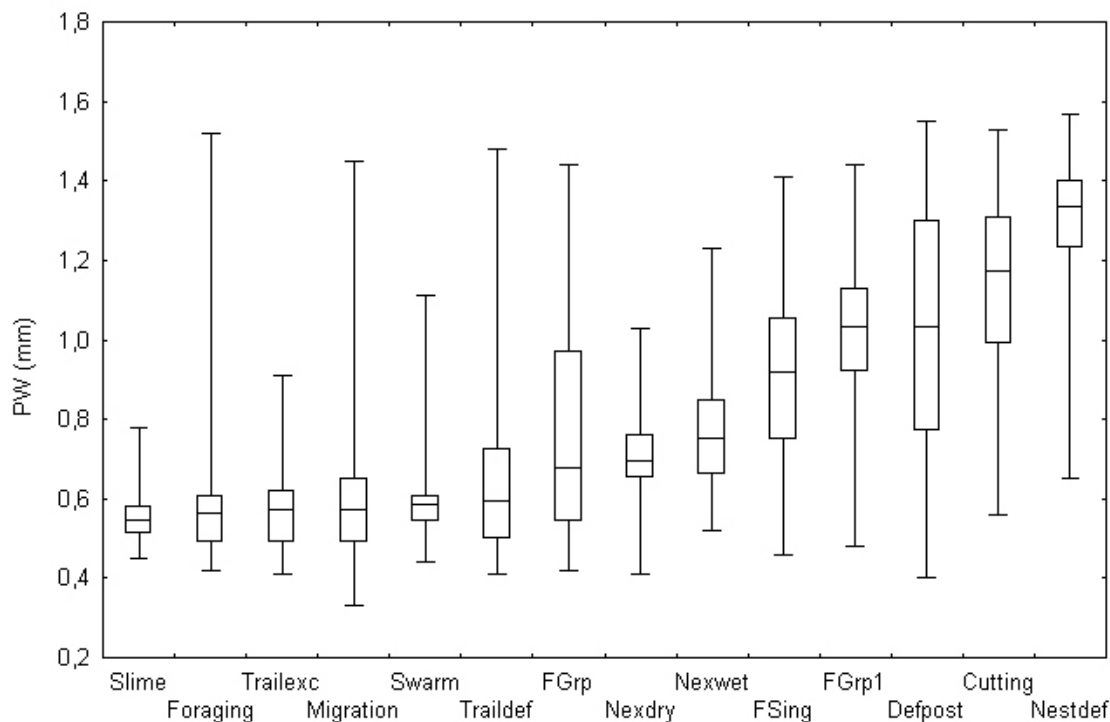


Fig. 7 Division of labour in *D. molestus*. Size of workers (measured as pronotum width) engaged in different tasks. The box encompasses the lower 25% and upper 75% percentile range; the internal line is the median; whiskers indicate the minimum and maximum values. The groups engaged in the various tasks are arranged according to increasing median values.

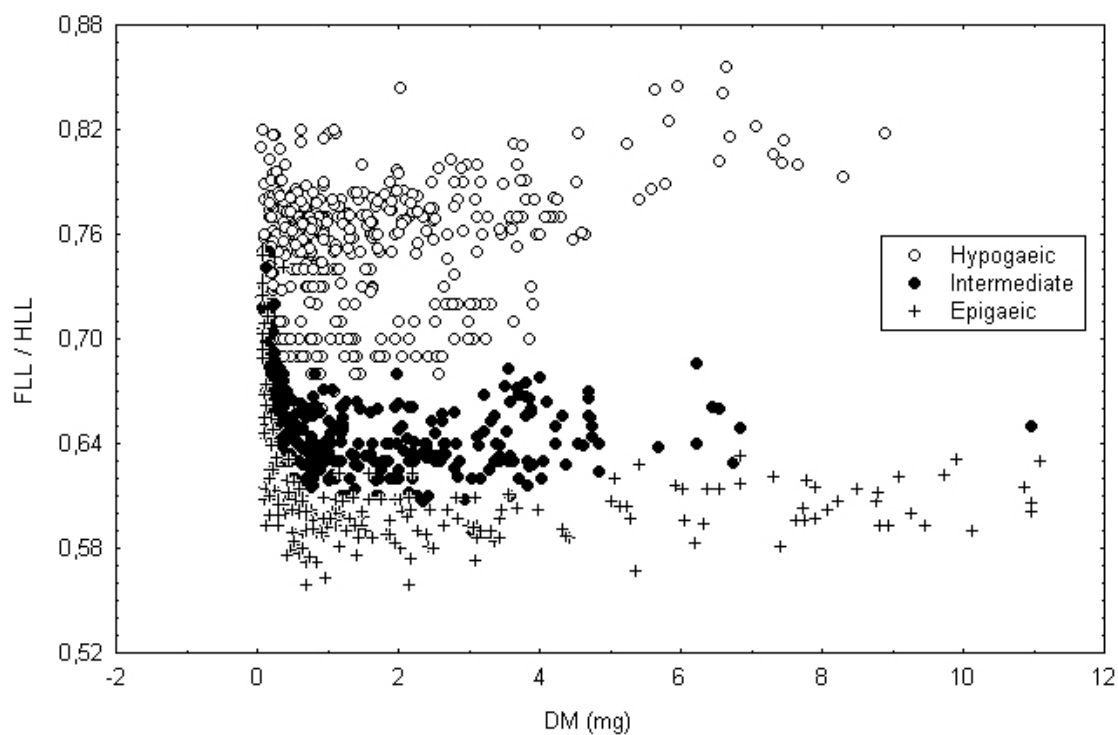


Fig. 8 FLL / HLL ratios vs. DM for workers of hypogaecic, intermediate and epigaeic species.

morphologies. As traits of identifiable functional value were selected for our morphometric analysis, we can try to pinpoint the selection pressures that may have favoured the morphological changes. For workers hunting in the leaf-litter and on the surface longer legs will convey advantages with respect to locomotion and food transport (i.e. they should be able to cover long foraging distances faster and / or more efficiently and carry more food mass per unit body mass, Franks 1985, 1986), and at the same time they will be much less constrained by the possible costs associated with longer (hind) legs than workers hunting in the soil. The leaf-litter stratum may also hold many interstices yet these will be on average larger than interstices in the soil simply because soil is more densely packed. The fact that the increase in hind leg length from hypogaecic to intermediate to epigaecic species is stronger than in front leg length with the effect that the ratio between front and hind leg length increases in the larger workers (dry mass > 1mg) from hypogaecic to epigaecic (see Fig. 8) indicates that food and/ or brood transport is indeed also of great importance for hypogaecic species but that longer hind legs are simply prohibitive for them when hunting in the soil. Longer legs and faster running speeds may in turn necessitate longer antennae to enable workers to follow the trail pheromone and / or avoid collisions with other workers running on the trail (Couzin and Franks 2003). Intermediate and epigaecic life-styles require more efficient defence as colonies will be more apparent to predators, more prone to disturbances during their raids and finally more vulnerable to thieves, in particular opportunistic birds which do not only catch animals escaping from the advancing swarm raid but also steal those that have been pinned down by the ants (C.S. pers. obs.). Longer mandibles, larger anterior head widths and as a result larger mandible gap widths should enable these species to inflict more painful bites on larger animals and thus pose a formidable deterrence. On the other hand, the features associated with locomotion and defence will also allow colonies to pin down and fragment larger prey animals. In summary, the inferred advantages associated with larger maximum head width, anterior head width, funiculus length, scape length, mandible length, mandible gap width, front and hind leg lengths are certainly complementary, but several of them can and should be tested. Large *D. molestus* workers (pronotum width > 0.9mm, this corresponds to a dry mass of about 1.6 mg) are disproportionately often engaged in food dismembering, food transport, and colony defence (see also Braendle et al. 2003), and a similar pattern can be found in *D. wilverthi* (Franks et al. 2001). As morphological differentiation among species is also more pronounced in workers of this size-class, this indicates that the requirement for efficiency in these tasks might have selected for divergent ecological niche specific morphologies.

According to the evolutionary scenario proposed by Gotwald (1978) the differences in life-style between extant *Dorylus* species are the result of a unidirectional shift from hypogaeic to epigaeic niches, but this scenario did not take into account more subtle differences in ecological niche use by *Anomma* species. Convergent evolution of similar characters is the strongest type of evidence for adaptation (Harvey and Pagel 1991). A species-level phylogeny of the genus *Dorylus* is lacking, and even the monophyly of *Dorylus s.str.* and *Anomma* are uncertain (Barr et al. 1985). Therefore, a more comprehensive analysis of morphological diversification will only be possible once the phylogeny of the genus has been established. Species in the army ant subfamilies Ecitoninae and Aenictinae also show prominent differences in their ecological niches (Rosciewski and Maschwitz 1994, Gotwald 1995) and therefore offer additional opportunities to examine the link between scaling relationships of the characters we have chosen and life-style.

The mechanisms allowing coexistence of different army ant species in a given habitat are poorly understood. Resource partitioning according to food item size has been shown to be an important mechanism in harvester ant assemblages (Davidson 1978) but is unlikely to be a relevant phenomenon here because hypogaeic, intermediate and epigaeic *Dorylus* spp. all display extensive polymorphism. Rather we suggest that species are using different strata of the same habitat for foraging and thereby reduce competition with each other. This however does not explain how different species displaying the same life-style can be sympatric.

Foraging stratum use is not completely static. During their swarm raids in the leaf litter workers of *D. opacus* and *D. emeryi* for example sometimes also come up to on the surface (but do not climb vegetation). On two occasions we observed antagonistic interactions between the epigaeic *D. wilverthi* and these two sympatric intermediate species. In both cases workers hunting in the leaf litter immediately withdrew to their usual hunting stratum into the leaf litter and into tunnels in the ground when the *D. wilverthi* swarm raids were approaching. This behaviour is different from the one displayed by colonies of the epigaeic species *D. molestus* during intraspecific encounters which simply continue the swarm raid in another direction (C.S. pers. observ.).