

PHYSICAL CASTES IN ANT WORKERS: A PROBLEM FOR
DACETON ARMIGERUM AND OTHER ANTS*

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INTRODUCTION

Morphological diversity among workers within ant colonies has its basis in allometry (Hölldobler and Wilson 1990). Physical castes (alternatively “subcastes”—often labelled minors, medias, and majors [soldiers] on the basis of size) have traditionally been defined with reference to peaks in the worker size-frequency distributions of polymorphic species.

According to Oster and Wilson (1978), *Daceton* has one of the most elaborate systems of physical castes among the ants. The only species in *Daceton*, *D. armigerum* (Fig. 1) is examined here in detail. We show that *Daceton* workers, though polymorphic, cannot be split into physical (sub)castes using multimodality in size-frequency curves and allometry (Wilson 1953). Application of the terms “caste” and “subcaste” to workers is critically reviewed.

MATERIALS, METHODS AND RESULTS

A *Daceton armigerum* colony was collected in its entirety on 6 May 1988 in the Imataca Forest Reserve, located east of El Palmar at the border between Bolivar State and Delta Amacuro Territory in Venezuela. The colony was large, with 2,342 workers. A sample of 132 foragers was collected separately in the field before we disturbed the nest. In addition a portion of the colony was taken alive for behavior studies by Hölldobler et al. (1990) and Moffett (in press). These samples were combined with previously preserved nest material prior to our overall analysis.

The worker size-frequency distribution was determined from head widths of an unbiased sample of a quarter of the colony by weight, amounting to 619 ants. There was only a singly clearly

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Fig. 1. *Daceton armigerum*: a range of worker sizes around brood in the nest.

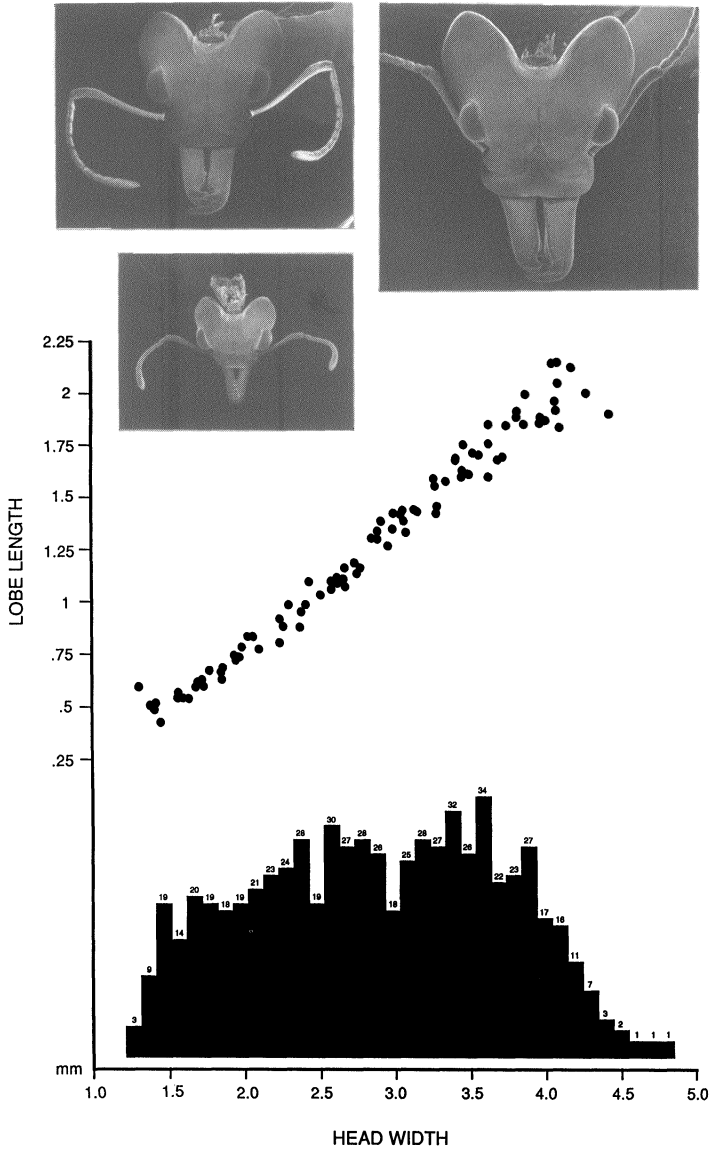
defined peak (Fig. 2), without any evidence of the skewing toward large size classes that results from developmental reprogramming for critical size in most highly polymorphic ants (Wheeler 1991).

The size-frequency distribution of adult workers is affected by size-related mortality factors (Calabi and Porter 1989). Worker pupae serve as better indicators of developmental mechanisms (Wheeler 1991). Preserved pupae from our colony tended to be crumpled, making measurements unreliable; however, roughly dividing the pupae into three size classes by eye indicated to us that they were probably similarly distributed in size to adults, with no skewing towards larger size classes.

Three measurements were made on 98 workers to the nearest 0.01 mm: 1) head width—maximum distance between the anterior margins of the eyes when viewed in perfect full face (Hölldobler and Wilson 1990); 2) distance between the tips of the humeral spines; and 3) distance from the posterior margin of the left eye to the most posterior reach of the temporal lobe on the same side of the head, with the head positioned in perfect full face view. Regressions between each pair of these characters, while nonisometric, were clearly linear—without any shifts in slope. Thus the allometry was consistently monophasic (Wilson 1953; Fig. 2), providing no basis for distinguishing subcastes.

DISCUSSION: WORKER CASTES—OR SUBCASTES?

The notion that workers of polymorphic species can be classified into “castes” or “subcastes” has been crucial to comparative studies of ant sociality. Yet when workers vary continuously in size, castes defined in terms of size-frequency distributions may not be comparable across taxa. Consider the rare size classes, which are typically used to delimit castes. These occur at the tails of a distribution, and, in species with multimodal size-frequency curves, at intermediate sizes. Such workers could be 1) suboptimal in performance, and so eventually might be lost entirely, as implied by Wilson's 1953 outline of the steps in caste evolution; 2)



uniquely functional in their own right (as in *Atta sexdens*: Wilson 1980) yet required in smaller numbers than adjacent size classes; or 3) serving the same roles as adjacent size classes, and with equal effectiveness—modality being merely a byproduct of the way worker birth or death rates relate to size. Furthermore, distributions are known to alter gradually yet dramatically as a colony grows in species such as *Solenopsis invicta* (Tschinkel 1988) and *Atta cephalotes* (Wilson 1983), or with diet (*Myrmecia*: Gray 1973) or season (*Messor pergandei*: Rissing 1987).

“Caste” and “subcaste” are usually treated as synonyms when describing worker size classes. However we propose that it would be more heuristic to use the term “caste” only for ants such as *Pheidole*, where the subdivisions are unambiguous. Such ants have worker size groups that are separated by distinct gaps, with workers of intermediate sizes being completely absent or so rare as to be considered anomalous. Contrast this with *Oecophylla*, in which intermediate-sized ants are rare but consistently present (Wilson 1953), as has been the case since the Miocene (Wilson and Taylor 1964). By our criteria, *Oecophylla* has one worker caste.

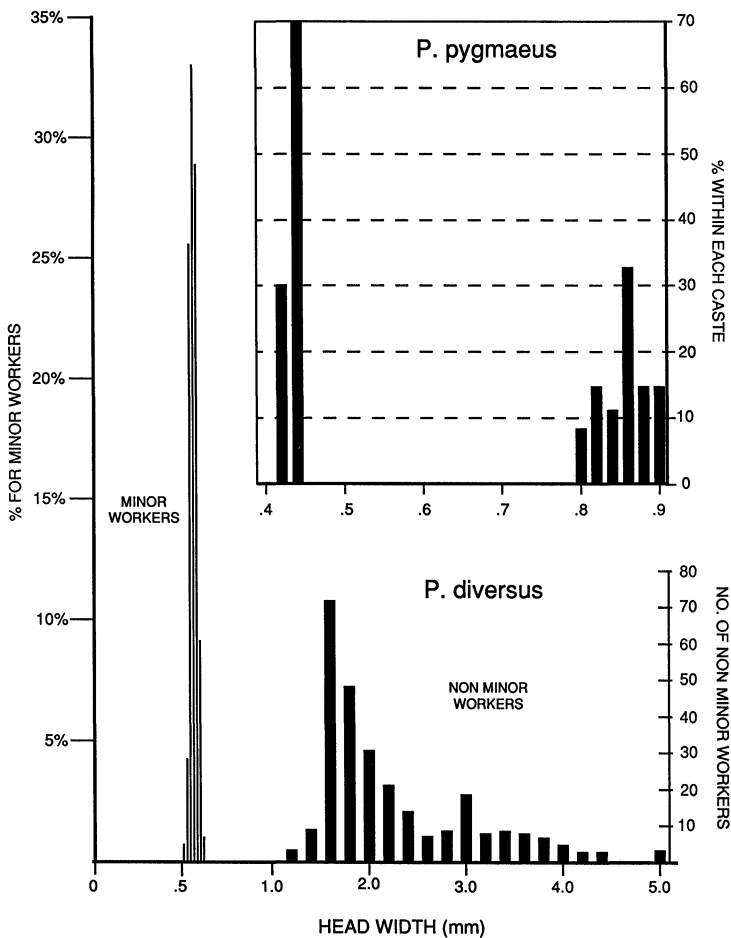
There are advantages to distinguishing disjunct worker size distributions from other examples of worker polymorphism. Individuals can be readily assigned to castes not only by size, but by obvious concomitant morphological features, such as head shape and sculpture. Also, the gaps are absolute and abruptly delimited even when narrow (e.g., Fig. 3). Thus the castes are certain to be sharply defined developmentally, though the underlying developmental rules (e.g., the reprogramming of growth and critical size: Wheeler 1991) may not be qualitatively different from those of continuous size distributions.

In addition, castes defined this way are behaviorally unique. Large size classes in particular often have special functions.

Fig. 2 (opposite). Worker allometry (head width vs. eye to occipital lobe distance: top) and worker size-frequency distribution (bottom) in a *Daceton armigerum* colony. While the species is clearly polymorphic (the slopes of allometric regression lines differ substantially from unity), worker allometry is consistently monophasic; in the example given, eye-lobe distance equals $-0.347 * (\text{Head width})^{0.592}$ with $r = 0.989$. Also, the size distribution is unimodal. Numbers in bar graph indicate numbers of ants of each head width in the sample. Scanning electron micrographs of minor, media and major worker subcastes are shown at identical magnifications.

Certain *Pheidole* species may be exceptions (Patel 1990) because majors have extremely broad behavioral repertoires that differ little from minors. We suggest, however, that these majors also serve specialized roles that have gone undetected.

“Subcaste” should be restricted to more artificial divisions of a size continuum. If subcastes are designated in terms of multimodality in the size-frequency distribution of full-grown colonies, only one of the four ant genera with species having an extreme



worker size variation (e.g., *Pheidologeton diversus*: Moffett 1987a) has two worker castes, one of which can be split into two or perhaps three subcastes (the complete worker size-frequency distribution of *P. diversus*, which has not been presented before in one figure, is shown with a discussion of the data in Fig. 3). *Eciton* (i.e., *E. burchelli*: Franks 1985) has one worker caste divisible into three or perhaps four physical subcastes. The other genera, *Atta* (Wilson 1980, 1983) and *Daceton*, have a single caste and no subcastes. An advantage of our terminology is that size distributions can be visualized more accurately without graphs.

While "caste" should have a precise definition, for instance to permit meaningful species comparisons, we prefer to keep the usage of "subcaste" flexible to distinguish size classes based on whatever physical or behavioral traits are convenient for a given species. Subcastes in *Daceton*, for example, might be delineated behaviorally. The foraging population consists almost entirely of ants with head widths of 2.2 mm or more (Fig. 4); anyone investigating polyethism would be well served to designate ants smaller than this as the minor worker subcaste (which carries out a preponderance of within-nest activities: Wilson 1962).

Such divisions are each researcher's prerogative; definitions could vary even between papers on one species (depending on convenience for the topic under discussion). For example, physical subcastes in *Atta* might be recognized on the basis of behavior or allometry, or defined in terms of hypotheses about the underlying developmental programs (as argued by Wheeler 1991).

Fig. 3 (opposite). Worker size-frequency distributions in a *Pheidologeton diversus* colony from Singapore (below and left) and a *P. pygmaeus* colony from Sarawak (top right). The wide size range of *P. diversus* nonminor workers probably arose from a narrowly defined major caste in a *P. pygmaeus*-like ancestor.

Measurements for the *P. diversus* colony were made on a sample of 1,080 minor workers and separately on a sample of 278 nonminors; the minor workers made up at least 99% of all workers in the colony, so if the minor worker peak was correctly proportioned on this page relative to the nonminors, the peak would be five meters tall! The largest worker in the whole colony was not in this sample (5.63 mm); the absolute gap of 0.46 mm between the largest minor and smallest nonminor was confirmed further for this colony by measurements of an additional 830 minors in the course of behavioral experiments prior to colony excavation.

Measurements for *P. pygmaeus* were made for 50 minors and 50 nonminors (majors)—the latter made up less than 0.5% of the worker labor force.

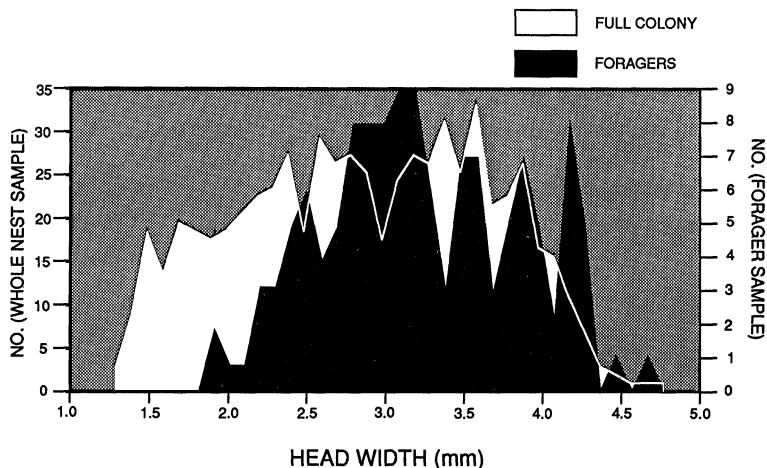


Fig. 4. Skewed distribution of foragers in *Daceton armigerum*. The forager sample showed a paucity of the smaller size classes, with 3% of the ants having head widths of 2.0 mm or less compared with over 22% for the colony as a whole.

Our discussion concerns physical caste systems. The delineation of temporal castes is another matter: we do not mind the use of “caste” to describe behaviorally distinct worker age groups—as long as the fact that the castes are temporal is made explicit. Wilson's (1976) distinction between discrete and continuous temporal caste systems, for example, remains invaluable.

Hölldobler and Wilson (1990) state that complete worker dimorphism (the presence of two distinct worker castes) has occurred “in no fewer than eight phylogenetically scattered genera.” Our altered definition of worker castes suggests a modified view, for, despite tremendous worker size variation (Fig. 3), isn't *Pheidologeton diversus* (like its congeners: Moffett, unpublished data) also in a sense dimorphic? Polymorphism in this genus most likely originated from the expansion of the major caste of an *Oligomyrmex*-like ancestor over an extreme size range, combined with the development of complex allometry (minor workers being largely unchanged). Indeed, the likely sister taxon to *Pheidologeton*, *P. pygmaeus* (which does not belong in *Pheidologeton*: Moffett 1987b), shows the exact ancestral condition we propose (Fig. 3).

Certain *Pheidole* have similar (though less extreme) polymorphisms to that of *Pheidologeton* workers (e.g., *P. bicarinata* and *P. subdentata*, Wheeler 1991). Close examination of other ants may reveal additional examples of such "mixed" caste systems.

In summary, we believe more care should be used in applying the terms "caste" and "subcaste" to worker populations within an ant colony. We recommend, in particular, that "caste" should be used only where there are disjunctions in worker size-frequency distributions and not for arbitrary subdivisions of a worker size continuum, as has been done in the past for the genus *Daceton*.

SUMMARY

Polymorphism in the South American arboreal ant *Daceton armigerum* is described and compared with that of other highly polymorphic ant species. The size-frequency distribution of *D. armigerum* workers is unimodal. Workers collected outside of the colony on foraging trails are also highly polymorphic but are considerably larger, on average, than the workers as a whole. An analysis of the relative size of various body parts shows that allometry in *D. armigerum* is monophasic. The use of the terms "caste" and "subcaste" in social insect biology is discussed, and unambiguous uses for these terms are proposed.

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