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Capitulo 4 : Castas: homología y analogía en la forma y función

Ant castes: homology and analogy in form and function

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Abstract

Ant societies consist of reproductive and sterile adults that show tremendous diversity of phenotypes. These include permanently wingless queens and a soldier caste that evolved convergently in many genera. Myrmecologists describe ant castes with terminology based on form, or function, or both, moreover terms are used inconsistently in the literature. Because morphology changes less readily than behaviour, an emphasis on morphological definitions is recommended to facilitate comparative studies and understand the evolutionary origin of castes.

All hymenopteran societies (except a few parasitic species) are composed of reproductives (sexual breeders) and sterile helpers. A majority of social bees and wasps (e.g. allodapines, halictids, polistines) have morphologically equivalent female adults that share the same larval development, and the division of labor between breeders and helpers is regulated by dominance interactions, insemination opportunities or age differences. In sharp contrast are other bees and wasps (*Apis*, *Bombus,* Meliponini, Vespidae) as well as all ants, where polyphenism (the development of alternative adult phenotypes from the same genotype) underlies the division breeding-helping. The terms "queen" and "worker" are commonly used to describe these distinct phenotypes, although some researchers use them merely to denote functional differences between breeders and helpers (see below).

All ant workers are wingless. The fundamental dichotomy between workers and winged queens can be conceptualized as a coupling of 'wingless' and 'sterility', as opposed to 'flight' coupled with 'reproduction'. Accordingly, the existence of wingless reproductives creates problems with terminology. Besides, the winglessness of ant helpers allowed a huge divergence in body size relative to winged queens, and this is unknown in social wasps and bees (Peeters & Ito 2015). Myrmecologists tend to forget this striking difference. The extent of morphological specialization breeder-helper is unparalleled in ants (in some termites, extreme physogastry of the queens results from ovarian physiology, not divergence during larval development; Beekman et al. 2006). Using consistent morphological terms gives due emphasis to this phenotypic divergence.

SEMANTICS AND MYRMECOLOGICAL JARGON

There is a long history of terms specific to the ant literature, starting with the numerous anomalies described by William Morton Wheeler (e.g. Wheeler 1937). Winglessness is the reason why ant castes (termites also!) give researchers considerably more headaches than the castes of social wasps and bees. Classification requires simple external traits in preference to hidden details. Flight ability is easily recognized from gross morphology (wings, and a complex thorax for attachment of wing muscles), but reproductive ability relates to function and thus behavioral observations or dissections are needed. Despite a lot of energy spent in semantic arguments during the last 100 years, the same terms continue to be used differently among researchers, and this prevents a unified terminology to help us understand ant diversity. Hölldobler & Wilson (1990) suggested to keep classification "somewhat loose, incorporating either anatomy or roles in a manner that maximizes convenience, precision, and clarity of expression". This means each one to his own, and I think this is not the best solution.

In this chapter I explain my point of view, because I was forced to think much about the meaning of terms during my career. I first studied ponerine ants in which the winged queens have been lost during evolution, and some of the workers reproduce sexually. What to call such mated egg-layers? I continued with the study of permanently wingless queens, which are now known in more than 70 ant genera (and counting...). More recently, I focused on developmental anomalies, and such 'intercastes' also challenge our definitions. I have tried to be consistent, but when new evidence became available, I did change my mind (see Box 1 of Peeters 2012). I am convinced that, unlike behavior, morphology gives us better information about caste evolution, because behavior is more liable to change. A morphological structure with a specific function evolves first, and later in evolution the function can change. Hence, form and function should not be given equal weight in comparative studies (Peeters & Crozier 1988). When members of the same morphological caste show behavioral changes over their lifespan, then additional descriptors of behavior or physiology (e.g. repletes) are needed, but I avoid "temporal castes" because there is danger of confusion with morphological castes.

Pragmatically, I urge to keep terms to a minimum. There are so many variants in caste differences in ants, each one does not require a special term! It is better to use fewer terms and to qualify them when appropriate. Importantly, this makes it less confusing for non-specialists, and helps outreach. But I was compelled to add jargon to the literature with the term 'gamergate'. In some ponerine ants, mated egg-laying workers differ from mated egg-laying queens (either ancestral or belonging to closely related species) in one crucial way: the ability to disperse and found a colony alone. As a PhD student, I was against calling them 'queens', and William (Bill) Brown coined the term 'gamergate' (married workers).

Semantic arguments can resemble religious ones because passions get involved. But unless we all agree to the same definitions, we cannot go forward and do comparative studies. This means that some of us need to change, although this should not be viewed as winning or losing. We are all winners if we use terminology in the same way, because it is a tool to help us decipher the marvelous diversity of the ant universe. I cannot resist taking the recent outburst of Baroni-Urbani (2015) as an illustration of the passions that divide myrmecologists: *".. erroneous, self-contradictory name i.e. 'winged queen' instead of the correct 'winged gyne'. Queen is a function, not a caste name and all ant queens are wingless, by definition*." I am not devoid of passion, but research on permanently wingless reproductives show these views to be archaic. Unlike Baroni-Urbani and others, I think the terms "queen" and "worker" must be strictly based on morphology (Peeters & Crozier 1988), because a remarkable divergence between breeding and helping phenotypes characterizes most ants.

Comparative studies need to distinguish between a common evolutionary origin (homology) and convergent/parallel evolution (analogy). Even though the degree of queen-worker dimorphism varies considerably across ants, winged queens have a uniform morphology (characteristic of a flying insect) due to shared ancestry. In contrast, ergatoid queens and soldiers evolved convergently in unrelated lineages having winged queens. They are grouped together as one broad category (mosaics of queen and worker traits; see below) although they do not have a single origin.

HOW TO DESCRIBE REPRODUCTIVES WITHOUT WINGS?

In ants, wingless reproductives can belong either to the queen caste (i.e. ergatoid queens) or the worker caste (i.e. gamergates). Reproductives that cannot fly are usually associated with a distinct strategy of colonial reproduction, i.e. there is a shift from independent to dependent colony foundation, e.g. Molet et al. 2009, Cronin et al. 2013.

1) ergatoid queens

Many terms in the literature describe permanently wingless female reproductives (summarized in Heinze 1998, Peeters 2012). The absence of wing muscles means that the thorax is reduced in volume, and many sclerites are fused together, hence ergatoid queens have a worker-like thorax. However, in many species their gaster is substantially larger than in workers, and this is consistent with greatly enhanced fecundity. Such ergatoid queens are often termed dichthadiiform when the gaster is huge, e.g. *Eciton, Simopelta*.

Molet et al. (2009) recognized two categories of ergatoid queens: (i) 'single-purpose' = few are produced in each colony, they are bigger than workers and function exclusively for reproduction, e.g. *Leptogenys*, *Monomorium algiricum*; (ii) 'multi-purpose' = many are produced in each colony, they are similar in size to workers, only one or few mate and reproduce while others remain virgin and function as labourers, e.g. *Mystrium oberthueri, Ocymyrmex*. Ergatoid queens are often described as intermediates between flying queens and workers, but it is more accurate to think of a <u>mosaic</u> (or patchwork) of queen and worker traits, e.g. highly specialized ovaries (queen-like trait) and simplified thorax (worker-like trait). In other words, gross comparisons of phenotypes are not helpful, or feasible, in ants. In the diagnosis of *Simopone,* Bolton & Fisher (2012) wrote "Known queens are entirely worker-like except that the mesosoma has a full complement of flight sclerites." Thus, conspecific queens and workers are highly similar in body size as well as thorax volume (flight thorax is little enlarged in most poneroids), however these queens can fly, a crucial trait affecting many life history traits.

Brachypterous (short-winged) queens also exist in many lineages, e.g. *Aphaenogaster araneoides, Cardiocondyla batesii, Cataglyphis velox, Lasius crypticus, Pogonomyrmex laticeps* (Peeters 2012, Peeters et al. 2012). Although wing muscles are lacking, the thorax of brachypterous queens is less simplified than in ergatoid queens, with most flight sclerites retained (Peeters et al. 2012). The short non-functional wings are often broken off within hours of adult emergence, and such dealate thorax can be mistaken for that of a flying queen (e.g. museum specimens). Like ergatoid queens, brachypterous queens are usually associated with colony fission (dependent colony foundation; Cronin et al. 2013). Thus they disperse on foot in the company of nestmate workers, and eliminating wing muscles makes them cheaper to manufacture.

2) gamergates

"Gamergate" is defined as a mated, egg-laying worker. It has a functional meaning, because all workers in a colony are morphologically equivalent (they all have a spermatheca). In some species, gamergates reproduce as well as a dealate queen, but in other species, the queens have been lost. In several species, many workers mate in each colony, but only a proportion lay eggs (e.g. *Harpegnathos saltator*). The mated workers with inactive ovaries are NOT gamergates. Thus, "gamergate" gives information on the physiology and behaviour of a given worker.

In some species, virgin workers lay unfertilized male-destined eggs, or trophic eggs - the latter are often just yolk sacs with abnormal chorion. These two functions are easy to distinguish from sexual reproduction performed by gamergates.

3) dealate mated queens

Some authors use ‘gyne’ to describe young winged queens that are still virgin – as opposed to ‘queens’ that are mated and dealate. Unfortunately, this can cause extra confusion, both for the general public and unspecialized scientists (‘gyne’ is additional myrmecological jargon), and even among specialists. Barry Bolton uses ‘queen’ and ‘gyne’ interchangeably, and even ‘dealate gyne’ (Bolton & Fisher 2012). This illustrates the pitfalls of a term that combines two traits: winged and virgin. Loss of wings is taken as evidence for mating status, but this is not always true, e.g. some queens fail to mate and shed their wings (see below). And what to call queens that emerge without wings? - they look the same irrespective of virgin or mated. Is it useful to write ‘ergatoid gynes’ when they are virgin?

Young ant queens that fail to disperse and mate can remain in the natal nest, shed the wings and function as helpers, e.g. *Acromyrmex echinatior, Ectatomma vizottoi,* and *Neoponera apicalis*. Hence they behave like the workers but only a morphological term can describe their developmental history and manufacturing costs. Describing them as ‘gyne’ is not useful, and it is necessary to specify ‘dealate virgin queens that behave like the workers’.

4) microgynes and macrogynes

This is a less confusing use of 'gyne' to distinguish between conspecific reproductive phenotypes differing in body size, e.g. *Ectatomma ruidum, Myrmica rubra, Temnothorax rugatulus*. Both can fly but they differ in dispersal and founding strategies. As mentioned earlier, dissections are needed to determine what individuals are mated and/or egg-laying.

5) flightless males

A very small number of ant species have wingless males. Consequent to the lack of wing muscles, the thorax is reduced in volume and sclerites fuse in some species. Hence "ergatoid" (worker-like) is appropriate to describe such males. However, in other species, wingless males retain flight sclerites, e.g. *Hagensia saldanhae* (Peeters & Robertson unpub.). In *Cardiocondyla, Metapone and Platythyrea*, ergatoid males have a large prothorax resulting from loss of wing muscles (Alpert 2007, Boudinot et al. 2016, Heinze et al. 2010). It is possible that such males have worker-like neck muscles, hence capable of carrying objects or fighting with other males (Boudinot et al. 2016, Heinze et al. 2010, Keller et al. 2014).

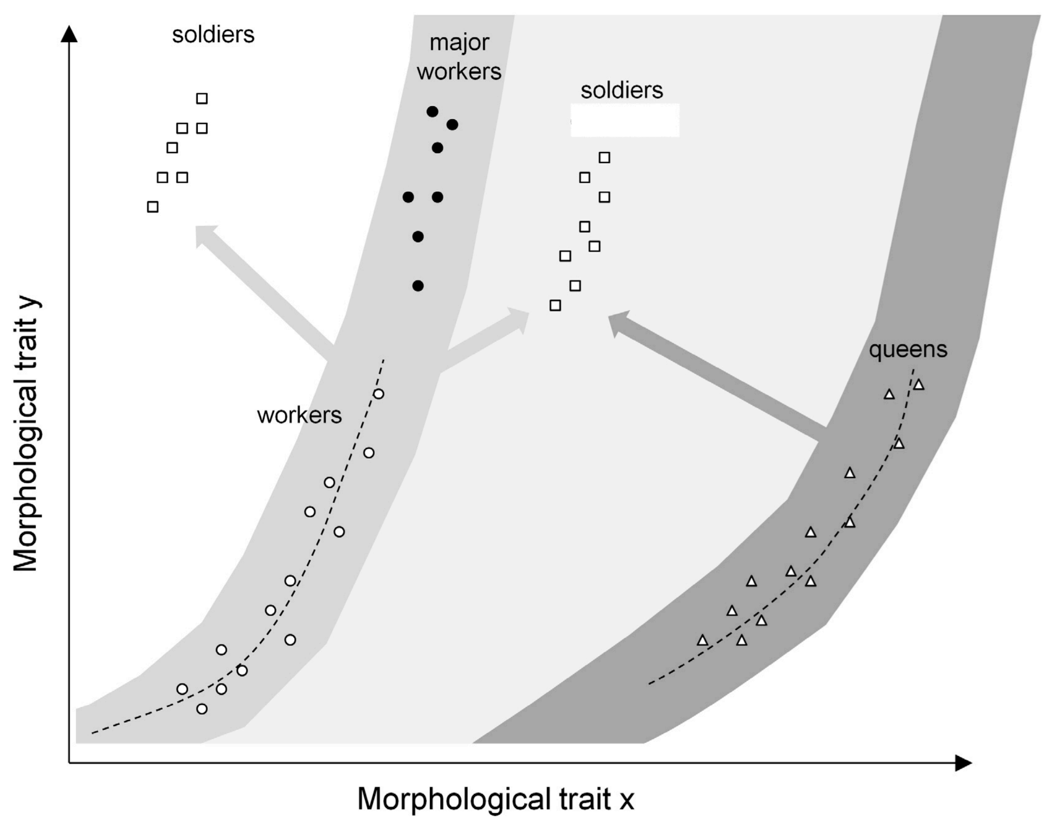
A THIRD CASTE : SOLDIERS

Unlike social wasps and bees, some ants have tiny workers occurring together with 'bigger helpers'. Bigger helpers often have huge heads that are packed with mandibular muscles. The prothorax is often enlarged because larger neck muscles are needed to support heavy heads (Keller et al. 2014). Gaster is generally bigger than in regular workers, and this is associated with food storage or production of trophic eggs. In some species, 'bigger helpers' are size-polymorphic workers (same growth rules but small and large individuals differ in shape due to allometry, e.g. many *Camponotus*). Other species have soldiers with morphological traits absent in workers, e.g. *Brachymyrmex, Carebara, Eciton, Pheidole* (discussed in Molet et al. 2014). Baroni-Urbani (2008) already made a distinction between 'soldiers' and 'major workers', whereby the latter's body proportions result from allometric growth within the frame of the worker developmental pathway (Fig. 1). Intra-colonial variability in helper size and shape evolved repeatedly across ant lineages, presumably driven by selection for cost-efficient specialization at various tasks. Confronted with this heterogeneity across lineages, it is important to distinguish between major workers and soldiers.

I suggest a broad definition for **soldiers: wingless sterile individuals with body size intermediate between ordinary workers and queens, and having traits that are absent in workers**. Soldiers are thus a third caste, neither workers nor queens. Their function varies strikingly between species and is not part of the definition, i.e. soldier is a strictly morphological term.

Historically, "soldier" was used because enlarged heads and mandibles seemed fit for defence. However larger mandibles can be specialized for seed-milling or wood-boring. Heads can be door-shaped (phragmotic) in *Cephalotes* and *Colobopsis*. A very important function of soldiers seems to be food storage. In several species, young soldiers behave as repletes, and as they get older they behave as guards. In *Crematogaster (Orthocrema)*, individuals with body size intermediate between huge queens and tiny workers exist. Their ovaries are specialized (same number of ovarioles as in queens) to lay trophic eggs, and they lack any defence function (Peeters et al. 2013). The term 'soldier' is appropriate to describe them because the underlying evolutionary mechanism appears similar to that occurring in other lineages with soldiers.

Fig. 1 Different adult castes exhibit distinct growth rules as illustrated (dashed lines) for a theoretical pair of morphological traits 'x' and 'y' in workers (empty circles) and queens (empty triangles). Growth rules combine 'growth rate' (speed at which each organ grows) and 'critical size' (larval body size at which growth stops and metamorphosis begins). Increasing critical size of worker larvae leads to larger adults that have a different shape due to allometry, i.e. major workers (black circles). However the range of possible phenotypes is limited (grey area surrounding the workers' curve). Alternatively, modifying both critical size and growth rate leads to novel adult phenotypes that are outside this range and accordingly do not belong to the worker caste, i.e. soldiers (empty squares). We suggest that either parameters of the growth rules of existing worker and queen castes can be combined, or new growth rules can evolve.
Taken from Molet et al. 2014



INTERCASTES: CLUES ABOUT THE EVOLUTIONARY ORIGIN OF ERGATOID QUEENS AND SOLDIERS

In the vast majority of ants with distinct morphological castes (queens and workers), aberrant queen-worker 'intercastes' occur occasionally (Peeters 1991, Heinze 1998, Molet et al. 2012), both in wild and laboratory conditions. Intercastes are intermediate in size between winged queens and workers, and their morphology is a mosaic of queen and worker traits. They can vary within species, ranging from very queen-like in thorax structure—though wings are absent or vestigial—to nearly worker-like. Importantly, a large gaster can occur without substantial development of thorax. Similarly, the reproductive organs vary. The highly variable morphology of intercastes in any given species provides valuable information about the integration of queen traits (e.g. ocelli, wings, complex segmentation of thorax, large gaster and ovaries, spermatheca) (Okada et al. 2013, Londe et al. 2015). Generally, such traits are all diminished or absent in workers. Intercastes are more likely (and more conspicuous) in species with a large difference in body size between queens and workers.

Intercastes are anomalous individuals produced erratically, and they should not be considered as a caste. Indeed, they are distinct from the regularly produced queens and workers. Moreover, intercastes are morphologically heterogeneous, at least in species where a sufficient sample has been examined. Counter-intuitively, these developmental accidents are not costly at colony-level. Intercastes are viable since they have survived to adulthood. They are diluted in a big colony, and many can function as laborers (albeit slightly less efficient than standard workers). Thus, selection against a low rate of developmental accidents is not expected. Intercastes exhibit novel phenotypes that are 'raw material' for evolution. For example, certain combinations of traits in intercastes can result in cheaper non-flying reproductives.

Intercastes express a mix of queen and worker developmental programs, resulting in a mosaic of queen and worker morphological traits. This makes them similar to ergatoid queens, but what are the differences?

- ergatoid queens are produced regularly (usually once a year), just like winged queens. They always have spermatheca, and in most species morphology is not variable (exceptions include *Myrmecina nipponica*). They mate with foreign males within colonies and lay eggs.

- intercastes are produced erratically and are rare. Some individuals have spermatheca and/or ovaries, but not others. Large colony series of specimens reveal great morphological variability, e.g. *Temnothorax nylanderi* (Okada et al. 2012) and *Mystrium oberthueri* (Londe et al. 2015). If ovaries and spermatheca are present, then intercastes can reproduce. However, the majority of intercastes behave just like workers. If a colony produces an intercaste having a useful novel function, then it can be selected and become produced regularly in this species (Molet et al. 2012). Alternatively, an intercaste may be cheaper (no wing muscles) and thus more cost-effective to perform an existing function.

Unless fresh material is available for dissection of ovaries, together with demography data from several complete colonies, it is difficult to assess differences between ergatoid queens and intercastes. Morphology can be the same. In rejection of Baroni-Urbani (2015)'s claim that our mosaic hypothesis is impossible to falsify, hence unscientific, Molet et al. (2012) discussed that it can be tested using comparative morphology as well as evo-devo, i.e. studying the expression of gene networks during development. This makes it possible to study what traits are shared (homologous) between reproductive and helper castes, and what traits are novel.

Researchers that come across anomalous ants in their colonies can contribute to a better understanding of this phenomenon by sending them for imaging at

http://www.antweb.org/intercastes. Images will be posted on AntWeb and specimens can be returned to you.

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