



HAL
open science

Castas: homología y analogía en la forma y función

Christian Peeters

► **To cite this version:**

Christian Peeters. Castas: homología y analogía en la forma y función. Fernando Fernández; Roberto Guerrero; Thibaut Delsinne. Hormigas de Colombia, Universidad Nacional Colombia, pp.159-164, 2019, 978-958-783-766-7. hal-02324626

HAL Id: hal-02324626

<https://hal.science/hal-02324626>

Submitted on 24 Oct 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



HORMIGAS DE COLOMBIA

F. Fernández, R.J. Guerrero & T. Delsinne
Editores

Instituto de Ciencias Naturales
Facultad de Ciencias
Sede Bogotá



UNIVERSIDAD
NACIONAL
DE COLOMBIA

TRANSLATION FROM SPANISH

Capítulo 6 *Castas: homología y analogía en la forma y función*

Hormigas de Colombia (2019) F. Fernández, R.J. Guerrero & T. Delsinne (editors). National University of Colombia pp. 159-164.

Ant castes: homology and analogy in form and function

Christian Peeters

*Institute of Ecology and Environmental Sciences, Sorbonne Université, CNRS,
4 place Jussieu, Paris, France*

christian.peeters@upmc.fr

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 between breeders and helpers in ants is unparalleled among social insects (in various 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 algericum*; (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 mosaic (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 echinator*, *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

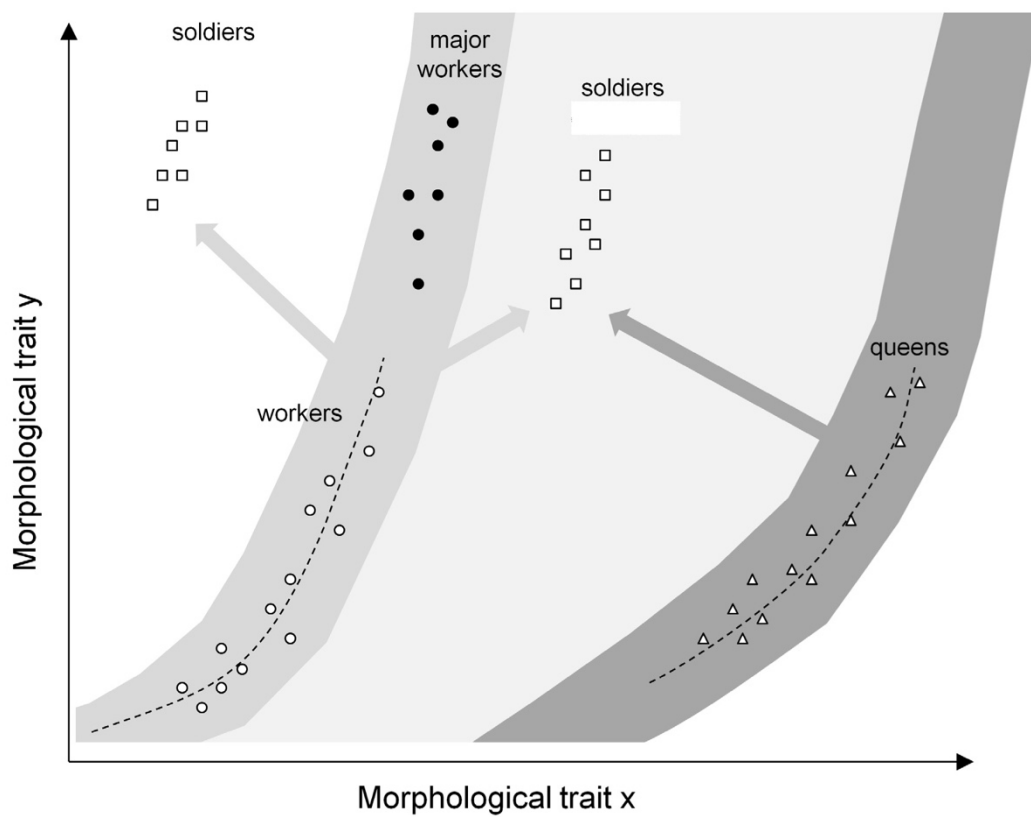
frame of the worker developmental pathway (Fig. 1). Intra-colonial variability in helper size and shape evolved repeatedly across ant lineages, presumably driven by selection for cost-efficient specialization at various tasks. Confronted with this heterogeneity across lineages, it is important to distinguish 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 nylander* (Okada et al. 2012) and *Mystridium 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 <https://www.antweb.org/project.do?name=anomalousants>. Images will be posted on AntWeb and specimens can be returned to you.

I thank Rodrigo Feitosa, Roberto Keller, Mathieu Molet, Thibaud Monnin, Rodolfo da Silva Probst, Thibaut Delsinne, Fernando Fernandez and an anonymous referee for helpful criticisms.

Literature cited

- Alpert, G.D. 2007. A review of the ant genus *Metapone* Forel from Madagascar. pp. 8–18 *In*: Advances in ant systematics (Hymenoptera: Formicidae): homage to E. O. Wilson – 50 years of contributions (eds Snelling RR, Fisher BL & Ward PS). Memoirs of the American Entomological Institute 80.
- Baroni Urbani, C. 1998. The number of castes in ants, where major is smaller than minor and queens wear the shield of the soldiers. *Insectes Sociaux* 45: 315-333.
- Baroni Urbani, C. 2015. Ant castes from intercastes: Much ado about nothing. *Sociobiology* 62: 328-330.
- Beekman, M., C. Peeters & O’Riain M.J. 2006. Developmental divergence: neglected variable in understanding the evolution of reproductive skew in social animals. *Behavioral Ecology* 17: 622-627.
- Bolton B. & B.L. Fischer 2012. Taxonomy of the cerapachyine ant genera *Simopone* Forel, *Vicinopone* gen. n. and *Tanipone* gen. n. (Hymenoptera: Formicidae). *Zootaxa* 3283: 1-101.
- Boudinot B.E., A.A. Wachkoo & H. Bharti 2016. The first ergatoid male of *Platythyrea* (Hymenoptera: Formicidae: Ponerinae), with contribution to colony labor suggested by observation and comparative morphology. *Myrmecological News* 22: 59-64.
- Cronin, A., M. Molet, C. Doums, T. Monnin & C. Peeters 2013. Recurrent evolution of dependent colony foundation across eusocial insects. *Annual Review of Entomology* 58: 37-55.
- Heinze, J. 1998. Intercastes, intermorphs, and ergatoid queens: Who is who in ant reproduction? *Insectes Sociaux* 45: 113-124.
- Heinze, J., Schmidt, C., Nugroho, H. & Seifert, B. 2010. Wingless fighter males in the Wallacean ant *Cardiocondyla nigrocerea* (Insecta: Formicidae). *Raffles Bulletin of Zoology* 58: 323-328.
- Keller, R.A., Peeters C. & Beldade P. 2014 Evolution of thorax architecture in ant castes highlights trade-off between flight and ground behaviors. *eLife* 3:e01539.

- Londe, S., Monnin, T., Cornette, R., Debat, V., Fisher, B. L. & Molet, M. 2015. Phenotypic plasticity and modularity allow for the production of novel mosaic phenotypes in ants. *Evodevo* 6, 36.
- Molet, M., B. Fisher, F. Ito & C. Peeters 2009. Shift from independent to dependent colony foundation and evolution of 'multi-purpose' ergatoid queens in *Mystrium* ants (subfamily Amblyoponinae). *Biological Journal of the Linnean Society* 98: 198-207.
- Molet, M., D. Wheeler & C. Peeters 2012. Evolution of novel mosaic castes in ants: Modularity, phenotypic plasticity, and colonial buffering. *The American Naturalist* 180: 328-341.
- Molet, M., V. Maicher & C. Peeters 2014. Bigger helpers in the ant *Cataglyphis bombycina* : Increased worker polymorphism or novel soldier caste? *PLoS ONE* 9(1): e84929.
- Okada, Y., L. Plateaux & C. Peeters 2013. Morphological variability of intercastes in the ant *Temnothorax nylanderi* : pattern of trait expression and modularity. *Insectes Sociaux* 60: 319-328.
- Peeters, C. 1991. Ergatoid queens and intercastes in ants: two distinct adult forms which look morphologically intermediate between workers and winged queens. *Insectes Sociaux*, 38: 1-15.
- Peeters, C. 2012. Convergent evolution of wingless reproductives across all subfamilies of ants, and sporadic loss of winged queens (Hymenoptera: Formicidae). *Myrmecological News* 16: 75-91.
- Peeters, C. & R.H. Crozier 1988. Caste and reproduction in ants: not all mated egg-layers are "queens". *Psyche* 95: 283-288.
- Peeters, C., R.A. Keller & R.A. Johnson 2012. Selection against aerial dispersal in ants: Two non-flying queen phenotypes in *Pogonomyrmex laticeps*. *PLoS ONE* 7(10): e47727.
- Peeters, C., Lin C.-C., Quinet Y., G. Martins Segundo & J. Billen 2013. Evolution of a soldier caste specialized to lay unfertilized eggs in *Crematogaster* ants (subgenus *Orthocrema*). *Arthropod Structure & Development* 42: 257-264.
- Peeters C. & Ito F. 2015. Wingless and dwarf workers underlie the ecological success of ants (Hymenoptera: Formicidae). *Myrmecological News* 21: 117-130.

Peeters, C. & M. Molet 2010. Colonial reproduction and life histories. pp. 159-176 *In: Ant Ecology* (eds L. Lach, C. Parr & K. Abbott). Oxford University Press.

Wheeler W.M. 1937. *Mosaics and other anomalies among ants*. Harvard University Press, Cambridge, MA

HORMIGAS DE COLOMBIA

F. Fernández, R.J. Guerrero & T. Delsinne
Editores



UNIVERSIDAD
NACIONAL
COLOMBIA

© Universidad Nacional de Colombia - Sede Bogotá
© Facultad de Ciencias
© Fernando Fernández (Ed. académico)
© Roberto Guerrero (Ed. académico)
© Thibaut Delsinne (Ed. académico)
© Autores varios

Primera edición, abril 2019

ISBN 978-958-783-765-0 (papel)

ISBN 978-958-783-766-7 (digital)

Facultad de Ciencias

Edición

Coordinación de Publicaciones
Facultad de Ciencias
coopub_fcbog@unal.edu.co

Diseño y diagramación

Valentina Nieto

Salvo cuando se especifica lo contrario, las figuras y tablas del presente volumen son propiedad de los autores

Bogotá, D. C., Colombia, 2019

Prohibida la reproducción total o parcial por cualquier medio sin la autorización escrita del titular de los derechos patrimoniales

Impreso y hecho en Bogotá, D. C., Colombia

Catalogación en la publicación Universidad Nacional de Colombia

Hormigas de Colombia / F. Fernández, R.J. Guerrero & T. Delsinne, editores. --
Primera edición. -- Bogotá : Universidad Nacional de Colombia. Facultad de
Ciencias. Instituto de Ciencias Naturales, 2019.
1200 páginas en dos columnas : ilustraciones (principalmente a color),
diagramas, fotografías, láminas

Incluye referencias bibliográficas al final de cada capítulo
ISBN 978-958-783-765-0 (rústica). -- ISBN 978-958-783-766-7 (e-book)

1. Formicidae 2. Hymenoptera 3. Taxonomía 4. Mirmecología 5. Región
neotropical 6. Biodiversidad 7. Colombia I. Fernández Castiblanco, Fernando,
1961-, editor II. Guerrero Flórez, Roberto José, 1981-, editor III. Delsinne,
Thibaut, 1978-, editor

CDD-23 595.796 / 2019

Contenido

Lista de autores	9
Lista de cuadros y figuras	11
Agradecimientos	25
Prólogo John E. Lattke	27
Presentación Jaime Aguirre	29
Capítulo 1. Hormigas de Colombia F. Fernández, R.J. Guerrero y T. Delsinne	31
Capítulo 2. Filogenia y sistemática de las hormigas neotropicales F. Fernández, R.J. Guerrero y T. Delsinne	57
Capítulo 3. Delimitación de especies en hormigas F. Fernández, R.J. Guerrero y T. Delsinne	91
Capítulo 4. Biología R.J. Guerrero, T. Delsinne y F. Fernández	121
Capítulo 5. Citogenética de las hormigas de la región neotropical C. dos S.F. Mariano, L.A.C. Barros, Y. Mera, I.N. Guimarães, S. das G. Pompolo y J.H.C. Delabie	131
Capítulo 6. Castas. Homología y analogía en la forma y función C. Peeters	159
Capítulo 7. Diversidad y morfología de las glándulas exocrinas en las hormigas J. Billen	165
Capítulo 8. Ecología I. Armbrrecht, P. Chacón de Ulloa, J. Montoya-Lerma, L.F. Rivera, G.A. Zabala, R. García-Cárdenas, M.C. Gallego-Ropero, J. Herrera-Rangel, N. Henao-Gallego, C. Sanabria, R.A. Achury, C. Santamaría, S. Escobar-Ramírez y E. Jiménez-Carmona.	175
Capítulo 9. Relaciones entre las hormigas y las plantas en los trópicos del Nuevo Mundo B. Corbara, C. Leroy, J. Orivel, A. Dejean y T. Delsinne	203
Capítulo 10. Parasitoides de hormigas P.J. Folgarait y A.C. Guillade	255
Capítulo 11. Métodos de recolección y curaduría R.J. Guerrero, T. Delsinne y W. Dekoninck	319
Capítulo 12. Manejo de datos O. Paknia	371
Capítulo 13. Glosario de morfología T. Delsinne, F.J. Serna, M. Leponce y B.E. Boudinot	387
Capítulo 14. Claves para las subfamilias y géneros F. Fernández, R.J. Guerrero y T. Delsinne	459
Capítulo 15. Clave para las subfamilias y géneros basada en machos B.E. Boudinot	487
Capítulo 16. Subfamilia Amblyoponinae F. Fernández, T. Delsinne y T.M. Arias-Penna	501
Capítulo 17. Subfamilia Ponerinae F. Fernández y R.J. Guerrero	509
Capítulo 18. Género <i>Hypoponera</i> S.T. Dash y W.P. Mackay	555
Capítulo 19. Subfamilia Dorylinae E.E. Palacio	571

Capítulo 20. Subfamilia Agroecomyrmecinae D.A. Donoso	631	Capítulo 30. Género <i>Pheidole</i> F.J. Serna, D. Suárez y A.L. Pérez	917
Capítulo 21. Subfamilia <i>Paraponerinae</i> T. Delsinne, G. Sonet y T.M. Arias-Penna	637	Capítulo 31. Género <i>Procryptocerus</i> F.J. Serna, W.P. Mackay y E.V. Vergara-Navarro	1055
Capítulo 22. Subfamilia <i>Ectatomminae</i> R.M. Feitosa y F.C. Prada-Achiardi	659	Capítulo 32. Género <i>Strumigenys</i> L.F. Pérez-Pedraza y F. Fernández	1069
Capítulo 23. Subfamilia <i>Proceratiinae</i> M.E. Escárraga, J.T. Longino y J. Sosa-Calvo	681	Capítulo 33. Subfamilia <i>Pseudomyrmecinae</i> P.S. Ward	1089
Capítulo 24. Subfamilia <i>Dolichoderinae</i> R.J. Guerrero	693	Capítulo 34. Hormigas de mayor impacto en la agricultura colombiana F.J. Serna, L.D. Mera-Rodríguez, K. Ramírez-Ossa y A. Gaigl	1115
Capítulo 25. Subfamilia <i>Formicinae</i> F. Fernández y C.M. Ortiz-Sepúlveda	721	Capítulo 35. Hormigas invasoras en Colombia W. Dekoninck, N. Wauters y T. Delsinne	1149
Capítulo 26. Género <i>Camponotus</i> W.P. Mackay y E. Mackay	743	Capítulo 36. Hormigas urbanas P. Chacón de Ulloa, J. Montoya-Lerma, J.C. Abadía, J. Rodríguez y K. Castaño-Quintana	1171
Capítulo 27. Subfamilia <i>Myrmicinae</i> F. Fernández y F.J. Serna	791	Capítulo 37. Galería de subfamilias y algunos géneros de hormigas de Colombia T. Delsinne, T.M. Arias-Penna, R.J. Guerrero y F. Fernández	1187
Capítulo 28. Género <i>Crematogaster</i> L. Pedraza y F. Fernández	889		
Capítulo 29. Género <i>Cephalotes</i> V.E. Sandoval-Gómez y A.F. Sánchez-Restrepo	899		

Lista de autores

JUAN C. ABADÍA

Departamento de Biología • Universidad del Valle •
Calle 13 # 100-00 Cali, Colombia • jcabadi@univalle.edu.co

RAFAEL A. ACHURY

Department of Entomology • University of Illinois at Urbana-Champaign • Urbana, Illinois, USA • Departamento de Biología • Universidad del Valle • Calle 13 # 100-00 Cali, Colombia • rafaelachury@gmail.com

TANIA M. ARIAS-PENNA

Les Pradeaux, France • tmilena@gmail.com

INGE ARMBRECHT

Departamento de Biología • Universidad del Valle • Calle 13 # 100-00 Cali, Colombia • inge.armbrecht@correounivalle.edu.co

LUÍSA A.C. BARROS

Departamento de Ciências Agrárias e Ambientais (DCAA) • Universidade Estadual de Santa Cruz (UESC) • KM. 16 rod Ilhéus-Itabuna • 45662-900 Ilhéus, Bahia, Brasil • luuvfv@yahoo.com.br

JOHAN BILLEN

Department of Biology • Lab. of Socioecology & Social Evolution • KU Leuven, Zoological Institute • Naamsestraat 59, box 2466, B-3000 Leuven, Belgium • johan.billen@kuleuven.be

BRENDON E. BOUDINOT

Department of Entomology & Nematology • University of California at Davis • One Shields Avenue • Davis, CA 95616, USA • boudinotb@gmail.com

KAREN CASTAÑO-QUINTANA

Departamento de Biología • Universidad del Valle •
Calle 13 # 100-00 Cali, Colombia • karenjq@gmail.com

PATRICIA CHACÓN DE ULLOA

Departamento de Biología • Universidad del Valle •
Calle 13 # 100-00 Cali, Colombia • patry.chacon@gmail.com

BRUNO CORBARA

Laboratoire Microorganismes: Génome et Environnement - LMGE • (CNRS / Université Blaise Pascal / Université d'Auvergne) • Université Blaise Pascal • Bât. Biologie A, 24 avenue des Landais, BP 80026, 63171 Aubière, France • bruno.corbara@univ-bpclermont.fr

SHAWN T. DASH

Assistant Professor of Biological Sciences • Hampton University • Hampton, Virginia, USA • Shawn.Dash@hamptonu.edu

ALAIN DEJEAN

CNRS, UMR EcoFoG, AgroParisTech, Cirad, INRA • Université des Antilles, Université de Guyane • 97310 Kourou, France • Alain.Dejean@ecofog.gf

WOUTER DEKONINCK

KBIN-IRSNB Dienst Patrimonium/Departement Entomologie • Curator Entomology Collections • Vautierstraat 29, 1000 Brussel, Belgium • wdekoninck@naturalsciences.be

JACQUES H.C. DELABIE

Departamento de Ciências Agrárias e Ambientais (DCAA) • Universidade Estadual de Santa Cruz (UESC) • KM. 16 rod Ilhéus-Itabuna • 45662-900 Ilhéus, Bahia, Brasil • Centro de Pesquisa do Cacao, CEPLAC • Ilhéus, Bahia, Brasil • jacques.delabie@gmail.com

THIBAUT DELSINNE

Société d'Histoire Naturelle Alcide-d'Orbigny • 57 rue de Gergovie • 63170 Aubière, France • tdelsinne@shnao.eu

DAVID A. DONOSO

Instituto de Ciencias Biológicas • Escuela Politécnica Nacional • Av. Ladrón de Guevara E11-253, Quito, Ecuador • david.donosov@gmail.com

MAYRON E. ESCÁRRAGA

Grupo de Investigación Insectos Neotropicales • Programa de Biología, Facultad de Ciencias Básicas • Universidad del Magdalena • Carrera 32 # 22-08 • Santa Marta, Colombia • mayronesneider@gmail.com

SELENE ESCOBAR-RAMÍREZ

Department of Crop Science • Universidad de Göttingen • Wilhelmsplatz 1, 37073 Göttingen, Alemania • Departamento de Biología • Universidad del Valle • Calle 13 # 100-00 Cali, Colombia • escobar.selene@gmail.com

RODRIGO M. FEITOSA

Departamento de Zoologia • Universidade Federal do Paraná • Caixa Postal 19020 • CEP 81531-980 • Curitiba - PR, Brasil • rsmfeitosa@gmail.com

FERNANDO FERNÁNDEZ

Profesor Asociado • Instituto de Ciencias Naturales • Universidad Nacional de Colombia • Carrera 30 No. 45 - 03 • Bogotá D.C. Colombia • ffernandezca@unal.edu.co

PATRICIA J. FOLGARAIT

Director Laboratorio Hormigas=ANTZ • Departamento de Ciencia y Tecnología • Universidad Nacional de Quilmes • Roque Saenz Peña 352, Bernal (B1876BXD), Bs As, Argentina • patricia.folgarait@gmail.com

ANDREAS GAIGL

Facultad de Ciencias Agrarias • Universidad Nacional de Colombia • Cra 30 # 45-03, Bogotá D.C., Colombia

MARÍA C. GALLEGU-ROPERO

Profesora titular • Departamento de Biología • Universidad del Cauca • Popayán, Cauca, Colombia • macrisgaro@yahoo.es

ROCÍO GARCÍA-CÁRDENAS

Departamento de Biología • Universidad del Valle •
Calle 13 # 100-00 Cali, Colombia • rociogarcia06

ROBERTO J. GUERRERO

Grupo de Investigación Insectos Neotropicales • Programa de Biología, Facultad de Ciencias Básicas • Universidad del Magdalena • Carrera 32 # 22-08 • Santa Marta, Colombia • rguerrero@unimagdalena.edu.co

ANDREA C. GUILLADE

Departamento de Ciencia y Tecnología • Universidad Nacional de Quilmes • Roque Sáenz Peña, Bernal 1876 • Argentina • andreaguillade@gmail.com

IASMYN N. GUIMARÃES

Universidade Estadual de Santa Cruz • Ilhéus, Bahia, Brasil • camponotu@hotmail.com

NATALIA HENAO-GALLEGO

Departamento de Biología • Universidad del Valle •
Calle 13 # 100-00 Cali, Colombia • natahenao@hotmail.com

JANINE HERRERA-RANGEL

Departamento de Biología • Universidad del Valle •
Calle 13 # 100-00 Cali, Colombia • ahera@gmail.com

ELIZABETH JIMÉNEZ-CARMONA

Departamento de Biología • Universidad del Valle •
Calle 13 # 100-00 Cali, Colombia • elizabethjimenez75@gmail.com

MAURICE LEPONCE

Biodiversity Monitoring & Assessment team leader • Aquatic & Terrestrial Ecology (ATECO) • Operational Directorate Nature • Royal Belgian Institute of Natural Sciences • 29 rue Vautier, 1000 Brussels, Belgium • maurice.leponce@naturalsciences.be

CÉLINE LEROY

IRD, UMR AMAP (botanique et Modélisation de l'Architecture des Plantes et des végétations) • Boulevard de la Lironde • TA A-51/PS2 • 34398 Montpellier Cedex 5, France • celine.leroy@ird.fr

JOHN T. LONGINO

Department of Biology • The University of Utah • Salt Lake City, UT 84112, USA • jacklongino@gmail.com

EMMA MACKAY
El Paso, Texas, USA.

WILLIAM P. MACKAY
Laboratory for Environmental Biology • Centennial Museum • University of Texas at El Paso • El Paso, TX 79968-0519, USA • wmackay@utep.edu

CLÉA DOS S.F. MARIANO
Departamento de Ciências Agrárias e Ambientais (DCAA) • Universidade Estadual de Santa Cruz (UESC) • KM. 16 rod Ilhéus-Itabuna • 45662-900 Ilhéus, Bahia, Brasil • csfmariano@gmail.com

LAURA D. MERA-RODRIGUEZ
Museo Entomológico UNAB • (Universidad Nacional Agronomía Bogotá) • Facultad de Ciencias Agrarias • Universidad Nacional de Colombia • Cra 30 # 45-03, Bogotá D.C., Colombia • ldmerar@unal.edu.co

YAMID MERA
Departamento de Ciências Agrárias e Ambientais (DCAA) • Universidade Estadual de Santa Cruz (UESC) • KM. 16 rod Ilhéus-Itabuna • 45662-900 Ilhéus - Bahia - Brasil • Universidad del Cauca • Cl. 5 #4-70 • Popayán, Cauca, Colombia • yamidml@gmail.com

JAMES MONTOYA-LERMA
Departamento de Biología • Universidad del Valle • Calle 13 # 100-00 Cali, Colombia • james.montoya@correounivalle.edu.co

CLAUDIA M. ORTIZ-SEPÚLVEDA
CNRS, Université de Lille • UMR 8198 Unité Evolution, Ecologie et Paléontologie • F-59000 Lille, France • claudiamarcelao@gmail.com

JÉRÔME ORIVEL
CNRS, UMR Ecologie des Forêts de Guyane • AgroParisTech, CIRAD, INRA, Université de Guyane • Université des Antilles, Campus Agronomique, BP316 • 97379 Kourou Cedex, France • orivel@cict.fr

OMID PAKNIA
Institute of Animal Ecology and Cell Biology • TiHo Hannover • Bünteweg 17d, Hannover 30559, Germany • omid.paknia@gmail.com

EDGAR E. PALACIO
ICA Barranquilla, Colombia • itoplectis@gmail.com

LINA PEDRAZA
Instituto de Ciencias Naturales • Universidad Nacional de Colombia • Carrera 30 No. 45 - 03 • Bogotá D.C., Colombia • limaria86@gmail.com

CHRISTIAN PEETERS
Institute of Ecology and Environmental Sciences • UMR CNRS 7618 • Université Pierre et Marie Curie • 4 Place Jussieu Paris 75005, France • christian.peeters@upmc.fr

LINA F. PÉREZ-PEDRAZA
Instituto de Ciencias Naturales • Universidad Nacional de Colombia • Carrera 30 No. 45 - 03 • Bogotá D.C., Colombia • lfperezp@unal.edu.co

ALBA L. PÉREZ
Museo Entomológico UNAB • (Universidad Nacional Agronomía Bogotá) • Facultad de Ciencias Agrarias • Universidad Nacional de Colombia • Cra 30 # 45-03, Bogotá D.C., Colombia • alperezbe@unal.edu.co

SILVIA DAS G. POMPOLO
Universidade Federal de Viçosa • Viçosa, Minas Gerais, Brasil • spompolo@ufv.br

FABIÁN C. PRADA-ACHIARDI
Instituto de Ciencias Naturales • Universidad Nacional de Colombia • Carrera 30 No. 45 - 03 • Bogotá D.C. Colombia • kaziell182@hotmail.com

KEVYN RAMÍREZ-OSSA
Museo Entomológico UNAB • Universidad Nacional Agronomía Bogotá • Facultad de Ciencias Agrarias • Universidad Nacional de Colombia • Cra 30 # 45-03, Bogotá D.C., Colombia • kevy_n_ramirez@ymail.com

LEONARDO F. RIVERA
Departamento de Biología • Universidad del Valle • Calle 13 # 100-00 Cali, Colombia • endimion_x@yahoo.com

JONATHAN RODRÍGUEZ
Departamento de Biología • Universidad del Valle • Calle 13 # 100-00 Cali, Colombia • Estudiante de Doutorado • Comportamento de insetos e semioquímicos • Laboratorio de Entomologia • UENF, RJ, Brasil. • nathan.rodriguez.g@gmail.com

CATALINA SANABRIA
Sciences de la Nature et de l'Homme: Evolution et Ecologie • Université Pierre et Marie Curie - Paris 6 • Paris, Francia • catasanabria@gmail.com

ANDRÉS F. SÁNCHEZ-RESTREPO
Becario doctoral Conicet. Fundación para el Estudio de Especies Invasivas (FuEDEL), Hurlingham, Buenos Aires, Argentina. • Grupo de Investigación en Filogenias Moleculares y Filogeografía (GIFF) • Departamento de Ecología, Genética y Evolución (EGE-FCEyN) • Universidad de Buenos Aires • Argentina • andrescp@gmail.com

VIVIAN E. SANDOVAL-GÓMEZ
Universidade Federal do Tocantins, campus Araguaína • Caixa Postal 1222 CEP, 77807-971 Araguaína, TO, Brasil • vivian.sandoval@gmail.com

CARLOS SANTAMARÍA
Departamento de Biología • Universidad del Valle • Calle 13 # 100-00 Cali, Colombia • csantave@gmail.com

FRANCISCO J. SERNA
Museo Entomológico UNAB • (Universidad Nacional Agronomía Bogotá) • Facultad de Ciencias Agrarias • Universidad Nacional de Colombia • Cra 30 # 45-03, Bogotá D.C., Colombia • fjsernac@unal.edu.co

GONTRAN SONET
Joint Experimental Molecular Unit • Direction Opérationnelle Taxonomie et Phylogénie • Royal Belgian Institute of Natural Sciences • 29 rue Vautier, 1000 Brussels, Belgium; • gontran.sonet@naturalsciences.be

JEFFREY SOSA-CALVO
Postdoctoral Research Fellow • Center for Social Insect Research, • School of Life Sciences, Arizona State University • 520 Orange St, Tempe, AZ 85281, USA • jsosacalvo@gmail.com

DIANA SUÁREZ
Museo Entomológico UNAB • Facultad de Ciencias Agrarias • Universidad Nacional de Colombia • Cra 30 # 45-03 • Bogotá, D.C. Colombia • dmsuarezg@unal.edu.co

ERIKA V. VERGARA-NAVARRO
Colección Taxonómica Nacional de Insectos "Luis María Murillo", Corpoica, Mosquera. • Museo Entomológico UNAB • Grupo Sistemática de Insectos Agronomía SIA • Facultad de Ciencias Agrarias • Universidad Nacional de Colombia • Cra 30 # 45-03 • Bogotá, D.C. Colombia • evvergar@unal.edu.co

PHILLIP S. WARD
Department of Entomology & Nematology • University of California at Davis • One Shields Avenue • Davis, CA 95616, USA • psward@ucdavis.edu

NINA WAUTERS
Brussels, Belgium • nina.wauters@gmail.com

GUSTAVO A. ZABALA
Departamento de Biología • Universidad del Valle • Calle 13 # 100-00 Cali, Colombia • gazant@gmail.com