REVIEW ARTICLE



On titles and royalty: a terminological discussion over castes in myrmecology

T. S. R. Silva¹ · R. M. Feitosa¹

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Abstract

Our knowledge of the processes related to the expression of distinct phenotypes in ants has significantly increased in the past few years. However, myrmecologists still face significant difficulties while addressing distinct patterns related to reproductive biology in ants. In the present work, we provide a theoretical discussion on the current limitations found in the process of caste representation in myrmecology, based on terminological theories. We also discuss how organizational frameworks can be valuable to logically represent classes related to reproductive biology and colonial tasks in ant societies. Hence, we provide a tentative terminology based on organizational structures to represent caste concepts.

Keywords Terminology · Ants · Reproductive biology · Concepts · Semiotics · Ontology · Form-function relationship

Introduction

During the history of myrmecology researchers have struggled to understand the behavioral and phenotypic patterns associated with reproduction and division of tasks in ants (Bolton 1986; Emery 1894; Molet et al. 2007; Peeters and Ito 2001; Wheeler 1905, 1991; Wilson 1953). Those struggles have arisen during the continuous exploration of reproductive strategies employed by these insects, with the discovery of deviant conditions. Apart from being considered challenges in the fields of evolution, physiology, and morphology, issues related to reproduction and colonial tasks have also been a nuisance in a terminological aspect, and myrmecologists have been faced with a long-lasting conundrum: "how to refer to such deviant patterns?".

Being a prolific and communicative group of researchers, much resembling their object of study, myrmecologists addressed questions regarding proper ways to refer to an ever-increasing number of reproductive and functional strategies that were being discovered in ants (Baroni Urbani

Historically, the use of terms to refer to distinctive reproductive and non-reproductive forms in myrmecology has always been a concern to researchers. The first attempt to clarify and organize all the knowledge obtained was made by Wheeler (1910), who provided a throughout representation of terms in an organizational structure, aiming to explicit the relations among the terminology applied at the time (Fig. 1), although not considering what type of relations these terms and their underlying concepts established with each other.

The establishment of terms for distinct forms was followed by Donisthorpe (1929), who was concerned with the description of distinct types of phenotypic mosaics, using agglutinations of terms previously established by Wheeler (1907) (e.g. ergatandromorph for individuals which expressed both apterous female and male morphological traits; and dinergatandromorph for specimens which expressed both "soldier" and male morphological traits). Some authors focused on reusing previously established concepts to define terms broadly used in social insects terminology under specific fields of knowledge. As an example, the term queens would be strictly defined as fertile females that participated in reproductive events (e.g. nuptial flights) for Buschinger and Winter (1976); and the same term would apply specifically to females having developed flight sclerites such as understood by Peeters and Crozier (1988). Some authors even applied terminologies that tried to combine

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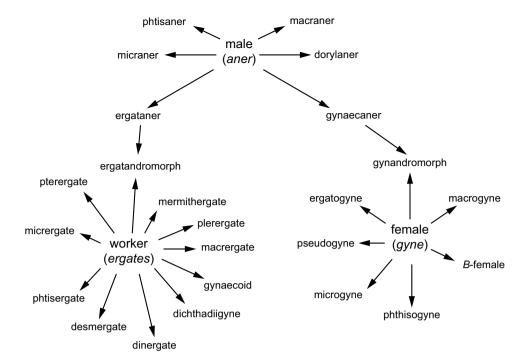


^{1998;} Peeters 1991, 2012; Heinze 1998; Hölldobler and Wilson 1990).

[☐] T. S. R. Silva tsranzanidasilva@gmail.com

Laboratório de Sistemática e Biologia de Formigas, Departamento de Zoologia, Universidade Federal do Paraná, Avenida Coronel Francisco Heráclito dos Santos, s/n, Curitiba 19020, Brazil

Fig. 1 One of the earlier schematic representation of terms used to refer to distinct forms ("castes") of ants. Adapted from Wheeler (1910)



distinct fields of knowledge to represent the distinct patterns found. For example, Buschinger (1987) proposed terms such as ergatomorphic queens (for apterous reproductive females) and gynomorphic workers (for infertile macropterous/brachypterous females) based on morphological and functional criteria.

Although firmly disagreeing with each other in some questions (Baroni Urbani 2015; Baroni Urbani and Passera 1996; Molet et al. 2012; Ward 1997), all the authors that addressed terminology issues in ant reproductive biology agreed that the ways that most terms were being applied were somewhat lacking in one or more aspects. While we are apparently walking on a road of mutual agreement, various aspects related to terminology have not been properly addressed, despite the efforts of researchers so far. Although terminology is known as a discipline that is concerned, basically, with setting terms, its primary concern is the study of concepts, conceptual systems, and their labels. Various aspects of terminology can be addressed using analytic tools, especially after the recent popularization of theories of terminology, concept theories and semiotics in fields such as knowledge representation (KR) and organization (KO) (Friedman and Thellefsen 2011), ontology (Thellefsen et al. 2018), and natural-language processing (Wiriyathammabhum et al. 2017). We believe that the myrmecological community can benefit from the ideas addressed in such fields to aim to a stabilization of terminology in ant reproductive biology, supported by a robust concept formulation, based on a relational concept structure.

In this paper, we discuss the advantages of applying principles of the semiotic theory in the logical reasoning for concept creation and how relational systems provide an operational framework in which concepts can be built and widely used in myrmecology. This particular part of the discussion is strongly influenced by Vogt's (2011) study of semiotics in biological sciences, and its critical reading is encouraged. We also explore some issues related to the creation of concepts in ant reproductive biology and functional morphology, especially regarding the form-function relationship premise (already briefly discussed in Peelers and Crozier 1988). We discuss some limitations that we face in the current method to represent castes in myrmecology and provide an alternative to conceptualize and reference them. We also propose a terminology based on an organizational structure, focusing on multi-domain conceptualization to highlight the positive aspects of this approach. More important than establishing a more or less lasting terminology in the literature, the concept which we are referring must be clear and unambiguous, enabling easier communication and, therefore, enhancing transparency and reproducibility, the hallmarks of science.

Materials and methods

A stand-alone organizational structure was developed using Protégé 5.2 (http://protege.stanford.edu/), an open-source ontology editor and a knowledge management system. Each entity is represented by a class (i.e. concept), a definition, class relationship types (i.e. indicating which type of relation occurs between two concepts; e.g. has_phenotype, causally_influenced_by) and class relationships (i.e. the record



Table 1 Preliminary class relationship types used in the development of the organizational structure for caste conceptualization

| Class relationship types | Definition |
|--------------------------|---|
| is_a | A transitive, reflexive and anti-symmetric relation between two or more entities |
| has_modifier | A relation that holds between an attribute or a qualifier and another attribute |
| has_phenotype | A relationship that holds between a biological entity and a phenotype. Here a phenotype is construed broadly as any kind of quality of an organism part, a collection of these qualities, or a change in quality or qualities (e.g. abnormally increased temperature) |
| causally_influenced_by | A relationship that holds between an attribute or qualifier and a process in which causality is involved, with either the attribute or qualifier exerting some influence over the process, or the process influencing some aspect of the attribute |

that links two concepts via a class relationship; e.g. "concept A has_phenotype concept B"). Class relationship types are based on the OBO Relations Ontology (RO 2018; version 11.vii.2018) (Table 1). Semantic annotations were manually added to continuant and occurrent entities within Protégé as OWL (Ontology Web Language) class expressions using the built-in Manchester syntax (http://www.w3.org/TR/owl2-manchester-syntax/) editor.

Preliminary data expressed in OWL are deposited in the Figshare Repository (https://doi.org/10.6084/m9.figsh are.6870080). The development of an unified, organizational structure for addressing caste terminology is at a preliminary stage of development and collaborative efforts are greatly encouraged; source codes and development logs can be accessed through GitHub's repository (CATO 2018).

Figures were expressed as vectors using Adobe Illustrator CS6® and exported as EPS (Encapsulated PostScript) files.

Results and discussion

Terminology, organizational framework, and ant castes

Terminology deals with the investigation, arrangement, and construction of terms and signs in general and the study of their use (Sonneveld and Loening 1993), covering the operations related to 1: (i) concept analysis; (ii) term identification assigned to concepts; (iii) establishment of correspondence, equivalence, opposition/contrast and conceptual dependences between terms; (iv) identification of ambiguous references between terms and their concepts; (v) compilation and organization of terms and their contents; (vi) and management of particular groups of terms. All these operations are related to the recording of terms, which function as signs, which in turn must be interpreted correctly to communicate semantic content.

In a logical and philosophical point, theories such as semiotics (cf. Vogt 2011 for a synopsis of the theory of semiotics) provides the means to understand how signs can evoke meaning in a perceiving mind, giving us tools for addressing the process of interpretation (Friedman and Thellefsen 2011). Although distinct proposals try to address different questions related to the representation of signs in different contexts under a general semiotics framework (Peirce 1992; Ogden and Richards 1952/1923), we still have issues referencing particulars and universals in biological sciences. However, much of its logical aspects can be beneficial for the study of concepts and terminology.

In this sense, a concept can be understood under a semiotic perspective as a textual or graphic representational artifact, which are human-made concretizations of cognitive representations of objects, processes, qualities, and states that exist in reality (Vogt 2011). Concepts can be systematized in an organizational framework named taxonomy. In this framework, concepts are organized in a class-subclass hierarchy; concepts are related to their subordinates in a top-down system (Fig. 2a). This system is useful to logically represent distinct levels of concepts within a certain domain of knowledge, also enabling a connection between different domains (Fig. 2b). Hence, they can be related to some extent; a certain class can be conceptualized using more than one axis of classification (Mungall et al. 2012). Using taxonomies for organizing terms can bring favorable effects since they draw the attention of users to the concepts that underlie the terms, and by visualizing categorical differences between terms, taxonomies can considerably facilitate consolidating conceptual consistency and categorical rigor (Vogt 2011).

In myrmecology, many terms used in reproductive biology refer to morphological variants that have distinct functions within the colony (Hölldobler and Wilson 1990; Peeters 2012). This is mostly a reflection of distinct concepts for the term caste. According to Hölldobler and Wilson (1990), three concept systems enclose the concepts of caste: physiological, physical, and temporal. For each system, there are subordinate concepts that are related to the

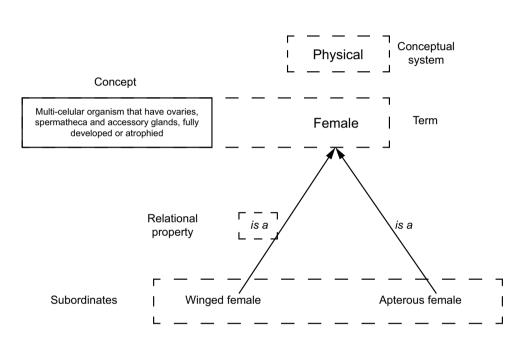


¹ Summarized by Vogt (2011).

Fig. 2 Different graphs representing different types of taxonomies. a A graphical representation of a taxonomy based on a unidirectional rule that allows for only one parent. b A graphical representation of a combinatorial taxonomy based on a unidirectional rule that allows for more than one parent. Modified from Vogt (2011)

A B

Fig. 3 Schematic relational structure of a conceptual system, which encloses concepts and their subordinates, their specific terms, and the relational properties connecting them



caste concept. In a physical system (Fig. 3), females can be defined as multi-cellular organisms that have ovaries, spermatheca and fully developed or atrophied accessory glands. In ants, there are winged and apterous individuals, which are terms that carry concepts related to the development of flight sclerites in the mesosoma. They can be considered as subordinate concepts connected to the female concept by a "is a" relational property.

In a physiological system, reproductive is an organismal quality in which an individual has the complete ability, partial ability or inability to produce new life or offspring. In ants, there are *sterile* (i.e. a reproductive quality in which the organism is incapable of initiating, sustaining, or supporting reproduction) and fertile (i.e. a reproductive quality in which the organism is capable of initiating, sustaining, or supporting reproduction) individuals. They are related to a reproductive quality through a "*is a*" relational property. For each concept, a term can be assigned. In ants, for example, apterous females are often called workers. There are terms,

however, that merge concepts from both systems: workers *are* apterous females and *are* sterile; queens *are* winged females and are fertile (Fig. 4).

Other terms refer to only one concept restricted to a conceptual domain. This occurs when we do not have the ability to establish if a particular organism is able to perform a specific behavioral role, or if it possesses a physiological condition, for example. In ants, we are not always able to determine if a winged female performs or not the oviposition behavior. In a discipline in which we routinely study deceased specimens, functional or physiological characteristics are difficult to observe. In these cases, a winged female is addressed as gyne (Fig. 5) (De Andrade and Baroni Urbani 1999; Wheeler 1908). Although much discussion has been made regarding the use of the terms gyne and queen to refer to winged females (Buschinger and Winter 1976, 1978; De Andrade and Baroni Urbani 1999; Peelers and Crozier 1988), they are mostly related to the distinct applications of conceptual systems applied by researchers to determine caste



Fig. 4 Schematic relational structure combining two distinct conceptual system, and the relation of the concepts between them

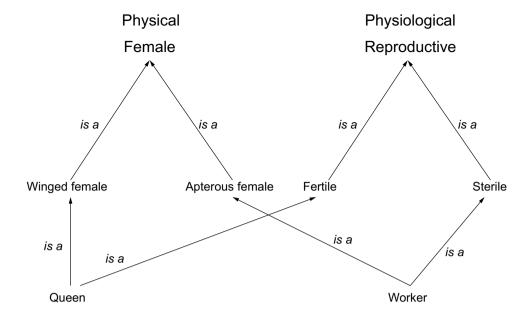
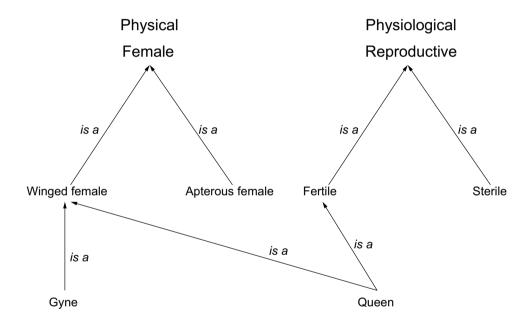


Fig. 5 Schematic relational structure combining two distinct conceptual system, and the conceptualization of concepts in a one-parent relation and two-parent relation



delimitation (e.g. purely physiological, purely morphological or morphological, physiological and behavioral).

During concept creation, we sometimes create incongruence due to logical inconsistencies when establishing parent-subordinate relations. Such conceptual issues can be observed when referring to groups of ants in which workers—presumably apterous sterile females—are capable of reproduction. Due to this deviant capacity, they receive the specific term *gamergates* (Peeters and Crewe 1985). In this case, two conflicting concepts (sterile and fertile) are used to categorize and term a class (Fig. 6a). This same condition appears in other groups of ants in which the queen—winged fertile females—are apterous. Due to their reduced structure

of the mesosoma, associated with their capacity of reproduction, they are called *ergatoid queens* (Peeters 2012). Once again, two conflicting concepts (winged and apterous) are used to categorize and term a class (Fig. 6b).

Although the developmental processes that originate both gamergates and ergatoids differ (Londe et al. 2015; Molet et al. 2012), the current ways to represent them are purely morphological and functional in nature. For each combination of concepts, researchers propose a new term, adding to an already extensive number of names. While the expression of phenotypic mosaics is seldom studied in most groups of Hymenoptera and in other social insects, researchers know that intrinsic and extrinsic processes determine the



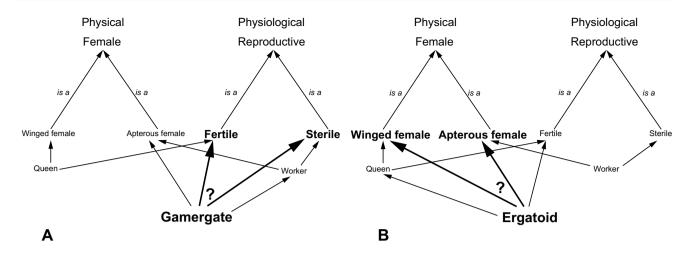


Fig. 6 Schematic relational structure combining two distinct conceptual systems, indicating subordinate concept incongruence derived from use of conflicting definitions during the conceptualization of an entity. a Concept incongruence of the gamergate subordinate, which

is related to apterous female, fertile and sterile (through worker parent). **b** Concept incongruence of the ergatoid subordinate, which is related to the winged female (through queen parent), apterous female and fertile. "?" indicates incongruence

expression of distinct phenotypes in an individual (Londe et al. 2015; Wheeler 1991) and, although distinct developmental components can be responsible for the expression of differential phenotypes within a single physical caste, the opposite can occur, and distinct developmental pathways can lead to the expression of similar phenotypes. If we consider all development options as means to enhance conceptualization of a class, we must bear in mind that they have to be unambiguous.

Another condition commonly found in species of ants is a morphological variant of a worker, that specializes in a function in the colony not related to reproduction and is mostly determined by behavior. This function can be related to the protection of the colony or of individuals of the same colony; to the obtention of resources through foraging; or to resource processing. In any of those cases, those workers are referred to as *soldiers* or *majors*. Although these terms have been used interchangeably in recent studies (Muscedere and Traniello 2012; Holley et al. 2016; Lillico-Ouachour and Abouheif 2017), various works (Baroni Urbani 1998; Baroni Urbani and Passera 1996; Molet et al. 2014) have discussed the striking differences between the concepts related to these terms, and their use remains elusive even today. However, it is mostly accepted that the term soldier should be loosely conceptualized as apterous sterile females that perform exclusively defensive roles in the colony (Baroni Urbani and Passera 1996).

There are other circumstances apart from the cited above in which workers are referred to as soldiers/majors, involving concepts from other conceptual domains (such as temporal/age domains). Similarly to the gamergates and ergatoids, the specialized behavior of these workers appears to be phylogenetic-constrained in some groups of ants while being environmental-constrained in others. The first case can be exemplified with soldiers belonging to different species of the genus Cephalotes Latreille, 1802, which have the sole purpose of defense of the colonial environment (Planqué et al. 2016). In contrast, the second case can be exemplified with soldiers or majors belonging to the genus *Pheidole* Westwood, 1839 (Holley et al. 2016; Lillico-Ouachour and Abouheif 2017), which can be responsible for the processing of trophic resource in some species whilst performing defensive behaviors in others (putatively performing both behaviors at the same time in some species belonging to this genus). The terms soldier and major are, then, used exclusively to refer to workers that perform defensive behaviors in some groups, while being used to refer to workers that can perform defensive, foraging and/or processing behaviors in other groups. This means that the term is dependent on the previous contextualization to be properly conceptualized, acquiring a polysemic condition based on this process (Fig. 7).

Different from the other terms discussed so far, the soldier/major discussion addressed above can be commonly found in the myrmecological literature. The same occurs with other terminological conflict related to the caste system: the concepts related to those terms should be understood under the caste concept, or they belong to a subcategory of it, collectively known as subcaste? Although tentatively establishing the differences between those concepts (Leniaud et al. 2015; Molet et al. 2014), the distinction between them cannot be promptly established in all groups of ants, in a uniform and unambiguous way, and, even to this day, confusion permeates these terms.

Although we are not aiming to the clear definition of what is or what may be an established concept of the terms



Fig. 7 Schematic relational structure combining three distinct conceptual systems, indicating subordinate concept incongruence derived from use of multiple context-dependent definitions during the conceptualization of an entity (i.e. polysemy). "?" indicates incongruence. Dashed lines indicate putative sufficient relation needed to conceptualize the entity

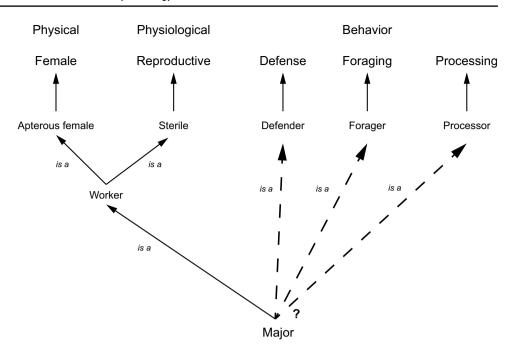
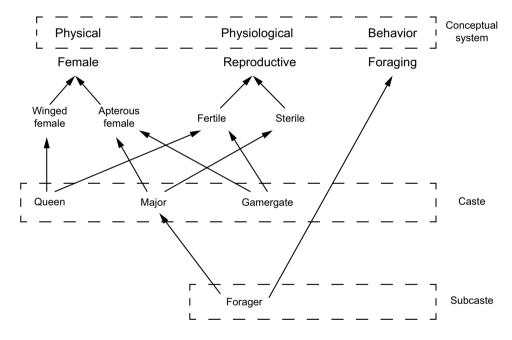


Fig. 8 Schematic relation used to tentatively assign caste and subcaste concepts, based on an organizational framework



caste and subcaste, and which concepts discussed above should be understood within them, we propose a conceptualization of these two terms under an organizational framework, to reinforce the idea that this method of reasoning can bring many advantages in the referencing process of patterns related to reproduction and colonial role in ants. Under this idea, a caste can be conceptualized as a realizable entity and it exists because there is some single bearer that is in some special physical, physiological, developmental and social set of circumstances in which this bearer

is conceived, and the caste is not such when the bearer ceases to exist. Hence any term conceptualized under two or more parent concepts (i.e. a set of circumstances) can be understood as a caste, while any term conceptualized under a caste concept can be understood as a subcaste (Fig. 8; *cf.* definition on Table 1). Although pragmatic at best, establishing specific thresholds for those terms can open doors to a more critical observation of the necessity to establish those limits, and, hence, helping to develop a more refined method to refer to these classes collectively.



Category mistake and the form-function relationship

According to Vogt (2011), biology suffers from terminology issues, which the author names the "linguistic problem of biology". Although much of the confusion pertaining to terminology in biology is centered in morphology, it is a problem of biology in general. Overall, the problems involving terminology (especially morphological) are characterized by Vogt et al. (2009) and summarized as: (i) semantic gap; (ii) terminology drift; (iii) category mistake; and (iv) overlap of descriptive data and explanatory hypothesis.

In the case of reproductive biology, we could consider that a lot of confusion relates to the lack of distinction between functional and anatomical terminology (Peelers and Crozier 1988). Based on the proposition of Vogt (2011), this would be considered a case of *category mistake* when dealing with caste terminology. The major issue concerning this question is that functional inferences are made based on structural sameness that is shared among different lineages, be they closely related or not. This idea is normally derived from one aspect related to semiotics and representation of natural signs (i.e. a sign that carries semantic content in virtue of some causal regularity or law), in which form–function relationship is considered an iconic representational index.

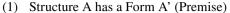
Iconic representational indices are natural mind-independent concretizations of putative cognitive representations (i.e. representations of entities in the form of ideas, thoughts, and beliefs in the mind of some cognitive subject) that function as natural iconic signs (Vogt 2011).

In the case of morphology, the anatomical class would theoretically function as an iconic representational index since it points to the function of a similar form, being based on an iconic resemblance of these two forms with the conclusion to a common function being based on analogy. However, the iconic resemblance of forms does not necessarily correspond to common function since the form–function relationship cannot be considered as an axiomatic statement—a causal relation—being rather a premise obtained through inductive reasoning.

Commonly, the form–function relationship can be logically represented as.

every form has a function, and every function is derived from a form.

When concerned with the study of causes and conditions involving each particular event, this premise gives us a starting point for the reasoning process, depending on the knowledge we have available and the intention of the study. Logically, it can be used in a deductive reasoning to reach a conclusion under a certain set of rules (*i.e.* conditions). As an example:



- (2) Either Form A' has a Function X or a Function Y (Premise)
- (3) If Form A' has a Function X, Structure A has a Function X (Premise)
- (4) If Form A' has a Function Y, Structure A has a Function Y (Premise)
- (5) Form A' do not execute Function X (Rule. Follows from 2 to 3)
- 6) Form A' execute Function Y (Rule. Follows from 2 to 4)
- (7) Form A' has a Function Y (Conclusion)
- (8) Structure A has a Function Y (Conclusion)

The issue with the extrapolation of the form-function relationship is that it is the construction of a premise, based on a premise; it applies inductive reasoning to establish a general cause, considering another general cause as a conclusion. As an example:

- (9) Structure B has a Form B' (Premise)
- (10) Either Form B' has a Function X or a Function Y (Premise)
- (11) If Form B' has a Function X, Structure B has a Function X (Premise)
- (12) If Form B' has a Function Y, Structure B has a Function Y (Premise)
- (13) Form B' is similar to Form A' (Premise)
- (14) Form B' has a Function Y (Conclusion. Follows 7)
- (15) Structure B has a Function Y (Conclusion. Follows 8)

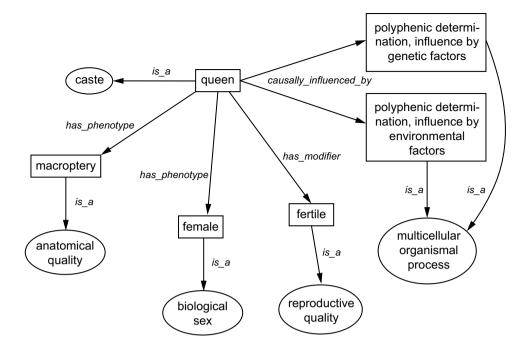
The conclusion observed in (14) and (15) would not be demonstrably true, since the rules (5) and (6), which were valid for Form A', were implicitly addressed in (13), disregarding that they may not be valid for Form B'.

An example of extrapolation of the form-function relationship in ants can be found in Silva and Brandão (2014). In this work, the authors observe variation in morphological aspects found in various specimens belonging to the myrmicine genera *Acanthognathus* Mayr, 1887 and *Strumigenys* Smith, 1860. In the study, the authors observed morphological mosaics between alate and apterous females in several specimens, assuming a putative reproductive role for the mosaics based solely on morphological criteria. In the case of ants, external morphology alone is not sufficient to infer reproductive aptitude since this characteristic is constrained by other aspects, such as physiological, behavioral and developmental conditions (Londe et al. 2015; Molet et al. 2012).

A cautionary approach must be taken when dealing with morphology and inferences of functionality. Although sometimes attractively intuitive, establishing causal relations based on the principle of analogy alone can lead to an incomplete understanding of the processes acting on the



Fig. 9 Organizational framework evidencing relations between occurrent and continuant entities, used in the process of referencing a queen concept



selection of different phenotypes, and hence, mistakes are made during the concept referencing process.

Application of organizational structures and multi-domain conceptualization in ant caste terminology

According to Peeters (2018), ant caste terminology should reflect pragmatic constructs through single-domain conceptualization; ant castes should be referenced solely through external morphological criteria. Although providing well-supported argumentation to his position through empirical means (e. g. Molet et al. 2009; Peeters and Ito 2015) and mentioning that morphology reflects better ant caste evolution, the author, during conceptualization, incorporates concepts from distinct domains to define much of the terms he suggests: single and multi-purpose ergatoids, gamergates, micro and macrogynes (differing in dispersal and founding strategies), etc. This inconsistency in domain definition for entity conceptualization, in this case, does not resolve incongruence in term usage.

The idea of terminology simplification through restriction of domain usage in the process of conceptualization inevitably leads to term stabilization. However, it also leads to oversimplification in the representation of things that exist in reality; this is especially true when we are dealing with the complexity inherited by ant societies.

Based on this, we tried to conceptualize some terms frequently used in the study of social division in ants, applying an organizational structure to establish relations with distinct concepts related to castes (Fig. 9). We focused on the use of distinct types of relation properties, to accurately establish

the specific relation between two or more concepts. We used both continuants (i.e. an entity that persists, endures, or continues to exist through time while maintaining its identity) and occurrent (i.e. an entity that unfolds itself in time or it is the instantaneous boundary of such an entity or it is a temporal or spatiotemporal region which such an entity) entities to conceptualize classes under a caste concept, providing a glossary to define terms referring to each entity (Table 2).

Conclusion

The factual application of a terminological proposition aiming for the reproducibility of concepts should be the focus of any endeavor concerned with stabilization of terms. However, this work does not aim to establish a new set of terms to represent differential behavioral or phenotypic patterns in the myrmecological literature. Terminological inconsistency is symptomatic of the pragmatism in term usage, without proper comprehension of subjacent conceptualization. We partially agree with Peeters (2018) when he refers to terminology as merely a tool to understand the complexity of ant societies. However, terminology is also a valid discipline of inquiry (as mentioned earlier in this study), concerned with the complex quality of ant societies, especially when we intend to represent all the knowledge obtained from its study.

Myrmecological history has shown us that, apart from the application of new terminologies, inconsistency and confusion still stands. We try, however, to show the importance of understanding and exploring the process of conceptualization, and how organizational structures, although not flawless, can ease our job in this process.



Table 2 List of terms and definitions used to refer to each entity, applying a multi-domain approach in the conceptualization process

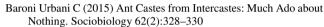
| Terms | Definition |
|------------|--|
| Caste | A realizable entity. It exists because there is some single bearer that is in some special physical, physiological, developmental and social set of circumstances in which this bearer is conceived. A caste is not such when the bearer ceases to exist |
| Ergatoid | A caste entity in which the bearer is apterous, fertile and which its polyphenic determination is influenced by genetic and environmental factors |
| Gamergate | A caste entity in which the bearer is female, apterous, fertile and which its polyphenic determination is influenced by genetic factors |
| Intercaste | A caste entity in which the bearer is female, a mosaic of distinct phenotypes and which its polyphenic determination is influenced by genetic and environmental factors |
| Major | A caste entity in which the bearer is female, apterous, sterile and which its polyphenic determination is influenced by genetic and environmental factors, and allometric growth rates |
| Queen | A caste entity in which the bearer is female, macropterous, fertile and which its polyphenic determination is influenced by genetic and environmental factors |
| Worker | A caste entity in which the bearer is female, apterous, sterile and which its polyphenic determination is influenced by genetic and environmental factors |
| Subcaste | A group of subordinate entities related to a parental caste entity exclusively through a behavioral quality |
| Forager | A subcaste entity in which the bearer is female, apterous, sterile and which its polyphenic determination is influenced by genetic and environmental factors, and allometric growth rates, performing exclusively foraging roles |
| Soldier | A caste entity in which the bearer is female, apterous, sterile and which its polyphenic determination is influenced by genetic and environmental factors, and allometric growth rates, performing exclusively direct or indirect defensive roles |

In this sense, the presentation of an idea focused on the comprehension of concepts is, currently, far more advantageous for myrmecology's terminology regarding reproductive biology and labor division. The use of organizational structures is an alternative to the discussion of concept representation outside established terminological schemas, logically allowing us to incorporate knowledge from distinct domains of inquiry during the process of representation. Trying to establish a new terminology based on this proposition, without the feedback of the myrmecological community, would not resolve the current representation issue; it would, however, add a new layer of inconsistency, reflected in the addition of differential term usage in the literature.

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References

Baroni Urbani C (1998) The number of castes in ants, where major is smaller than minor and queens wear the shield of the soldiers. Insect Soc 45(3):315–333



Baroni Urbani CB, Passera L (1996) Origin of ant soldiers. Nature 383(6597):223

Buschinger A (1987) Polymorphism and reproductive division of labor in advanced ants. In: Eder J, Rembold H (eds) Chemistry and biology of social insects. Verlag J. Peperny, Munich

Buschinger A, Winter U (1976) Funktionelle Monogynie bei der Gastameise *Formicoxenus nitidulus* (NYL.) (Hym., Form.). Insect Soc 23:549–558

Buschinger A, Winter U (1978) Echte Arbeiterinnen, fertile Arbeiterinnen und sterile Wirtsweibchen in Völkern der dulotischen Ameise *Harpagoxenus sublaevis* (NYL.) (Hym., Form.). Insect Soc 25:63–78

Bolton B (1986) Apterous females and shift of dispersal strategy in the *Monomorium salomonis*-group (Hymenoptera: Formicidae). J Nat Hist 20(2):267–272

CATO (2018) Repository for the Caste Ontology development https://github.com/feitosalab/cato. Accessed 26 July 2018. https://doi.org/10.5281/zenodo.1322125

De Andrade ML, Baroni Urbani C (1999) Diversity and adaptation in the ant genus *Cephalotes*, past and present. Stutt Beitr Naturkd B 271:1–889

Donisthorpe H S J K (1929) Gynandromorphism in ants. Zoologischer Anzeiger 82:92–96

Emery C (1894) Die Entstehung und Ausbildung des Arbeiterstandes bei den Ameisen. Biol Zent Bl 14:53–59

Friedman A, Thellefsen M (2011) Concept theory and semiotics in knowledge organization. J Doc 67(4):644–674

Heinze J (1998) Intercastes, intermorphs, and ergatoid queens: who is who in ant reproduction? Insect Soc 45(2):113–124

Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge

Holley JAC, Moreau CS, Laird JG, Suarez AV (2016) Subcaste-specific evolution of head size in the ant genus *Pheidole*. Biol J Linn Soc Lond 118(3):472–485

Leniaud L, Pearcy M, Taheri A, Aron S (2015) Testing the genetic determination of the soldier caste in the silver ant. Insect Soc 62(4):517–524



- Lillico-Ouachour A, Abouheif E (2017) Regulation, development, and evolution of caste ratios in the hyperdiverse ant genus *Pheidole*. Curr Opin Insect Sci 19:43–51
- Londe S, Monnin T, Cornette R, Debat V, Fisher BL, Molet M (2015)

 Phenotypic plasticity and modularity allow for the production of novel mosaic phenotypes in ants. Evodevo 6(1):36
- Molet M, Fisher B, Ito F, Peeters C (2009) Shift from independent to dependent colony foundation and evolution of 'multi-purpose' ergatoid queens in *Mystrium* ants (subfamily Amblyoponinae). Biol J Linn Soc 98:198–207
- Molet M, Maicher V, Peeters C (2014) Bigger helpers in the ant *Cataglyphis bombycina*: increased worker polymorphism or novel soldier caste? PLoS One 9(1):e84929
- Molet M, Peeters C, Fisher BL (2007) Winged queens replaced by reproductives smaller than workers in *Mystrium* ants. Naturwissenschaften 94(4):280–287
- Molet M, Wheeler DE, Peeters C (2012) Evolution of novel mosaic castes in ants: modularity, phenotypic plasticity, and colonial buffering. Am Nat 180(3):328–341
- Mungall CJ, Torniai C, Gkoutos GV, Lewis SE, Haendel MA (2012) Uberon, an integrative multi-species anatomy ontology. Genome Biol 13(1):R5
- Muscedere ML, Traniello JF (2012) Division of labor in the hyperdiverse ant genus *Pheidole* is associated with distinct subcasteand age-related patterns of worker brain organization. PLoS One 7(2):e31618
- Ogden CK, Richards IA (1952/1923) The meaning of meaning: a study of the influence of language upon thought and the science of symbolism. Harcourt, Brace & World Inc., New York
- Peeters C (1991) Ergatoid queens and intercastes in ants: two distinct adult forms which look morphologically intermediate between workers and winged queens. Insect Soc 38(1):1–15
- Peeters C (2012) Convergent evolution of wingless reproductives across all subfamilies of ants, and sporadic loss of winged queens (Hymenoptera: Formicidae). Myrmecol News 16:75–91
- Peeters C (2018) Ant castes: homology and analogy in form and function (Version March 2017). Zenodo. https://doi.org/10.5281/zenodo.1215470
- Peeters C, Crewe R (1985) Worker reproduction in the ponerine ant *Ophthalmopone berthoudi*: an alternative form of eusocial organization. Behav Ecol Sociobiol 18(1):29–37
- Peeters C, Crozier RH (1988) Caste and reproduction in ants: not all mated egg-layers are "queens". Psyche (Stuttg) 95(3-4):283-288
- Peeters C, Ito F (2001) Colony dispersal and the evolution of queen morphology in social Hymenoptera. Annu Rev Entomol 46(1):601–630
- Peeters C, Ito F (2015) Wingless and dwarf workers underlie the ecological success of ants (Hymenoptera: Formicidae). Myrmecol News 21:117–130

- Peirce CS (1992) The essential peirce: selected philosophical writings, vol 2. Indiana University Press, Bloomington
- Planqué R, Powell S, Franks NR, Berg JB (2016) Disruptive selection as a driver of evolutionary branching and caste evolution in social insects. J Evol Biol 29(11):2111–2128
- RO (2018) Repository for the relations ontology. https://github.com/ oborel/obo-relations. Accessed 11 July 2018
- Seltmann KC, Yoder MJ, Miko I, Forshage M, Bertone MA, ... Deans AR (2012) A hymenopterists' guide to the hymenoptera anatomy ontology: utility, clarification, and future directions. J Hymenopt Res 27:67–88
- Seltmann KC, Pénzes Z, Yoder MJ, Bertone MA, Deans AR (2013) Utilizing descriptive statements from the biodiversity heritage library to expand the hymenoptera anatomy ontology. PLoS One 8(2):e55674
- Silva TSR, Brandão CRF (2014) Further ergatoid gyne records in the ant tribe Dacetini (Formicidae: Myrmicinae). Neotrop Entomol 43(2):161–171
- Sonneveld HB, Loening KL (1993) Terminology: applications in interdisciplinary communication. John Benjamins Publishing, Amsterdam
- Thellefsen MM, Thellefsen T, Sørensen B (2018) Information as signs: a semiotic analysis of the information concept, determining its ontological and epistemological foundations. J Doc 74(2):372–382
- Vogt L (2011) Signs and terminology: science caught between language and perception. Bionomina 4:1–41
- Vogt L, Bartolomaeus T, Giribet G (2010) The linguistic problem of morphology: structure versus homology and the standardization of morphological data. Cladistics 26(3):301–325
- Ward PS (1997) Ant soldiers are not modified queens. Nature 385(6616):494
- Wheeler DE (1991) The developmental basis of worker caste polymorphism in ants. Am Nat 138(5):1218–1238
- Wheeler WM (1905) Worker ants with vestiges of wings. Bull Am Mus Nat Hist 21:405–408
- Wheeler WM (1907) The polymorphism of ants, with anaccount of some singular abnormalities due to parasitism. Bull Am Mus Nat Hist 23:1–93
- Wheeler WM (1908) The polymorphism of ants. Ann Entomol Soc Am 1:39-69
- Wheeler WM (1910) Ants: their structure, development and behavior. Columbia University Press, New York
- Wilson EO (1953) The origin and evolution of polymorphism in ants. Q Rev Biol 28(2):136–156
- Wiriyathammabhum P, Summers-Stay D, Fermüller C, Aloimonos Y (2017) Computer vision and natural language processing: recent approaches in multimedia and robotics. ACM Comput Surv 49(4):71

