

Definitions of «caste» in social insects

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Definitions of *caste* must be based on either form or function, since the combination of both in a single definition makes the concept impossible to apply in many cases. Developmental, functional and evolutionary studies gain heuristically from a distinction between the form and the social role of a social insect, which means that the two should be treated as conceptually distinct.

Caste has traditionally denoted the physical form of a social insect. The term *role* can describe the social function of an insect in its colony, and an associated descriptive terminology already exists. Defining *caste* to denote only social function requires extensive changes to this terminology. It is therefore proposed that *caste* should be defined to mean groups of individuals sharing a common, discrete morphogenetic pathway only. The application and heuristic value of this approach are discussed.

KEY WORDS: caste, role, form, function, morphogenesis, ethogenesis, ontogeny, Hymenoptera, Isoptera.

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INTRODUCTION

As knowledge of any subject grows, it can become necessary to refine or replace the underlying concepts and the terms relating to them. The concept of *caste*, a pivotal notion in studies of sociality in insects, has become such a confused issue that it formed the topic of a special symposium (BUSCHINGER & CROZIER 1987) at the Tenth International Congress of the International Union for the Study of Social Insects,

held in München, late in 1986. It is clear from the contributions to that congress (EDER & REMBOLD 1987) and recent reviews (NOIROT & PASTEELS 1987, ENGELS 1990, HÖLLDOBLER & WILSON 1990), that *caste* is understood to imply different concepts in different groups of insects. The most recent authoritative, formal definition of *caste* is «any set of individuals of a particular morphological type or age group, or both, that performs specialized labour in the colony. More narrowly defined, any set of individuals in a given colony that is both morphologically distinct and specialized in behaviour» (HÖLLDOBLER & WILSON 1990: 636).

This perspective has existed formally for over two decades (WILSON 1968). However, WILSON (1984), WHEELER (1986), CALABI (1988) and others have shown that behaviour and morphology are uncoupled phenomena in social insects. JEANNE (1986) discussed important differences between their implications. BUSCHINGER (1987, 1990), following MICHENER (1974), proposed that the concept of *caste* should connote only functional differences between members of a colony, with an implicit emphasis on reproductive function. The following year, PEETERS & CROZIER (1988) put forward a counter-argument for limiting it to morpho-anatomical differences, in order to clarify issues in the reproductive biology of ants. More recently still, it was suggested that the concept was no longer useful (GORDON 1989).

The concept of *caste* has been used not only in reproductive biology, but also in insect physiology, embryology, behavioural ecology and evolutionary theory, and it would be valuable to unify the terminology of these areas of social biology (BUSCHINGER & CROZIER 1987), even if the concept is later discarded. The following discussion reviews evidence that the form and function of colony members are separate, although related, properties. The terminology available for thinking about these concepts is explored, and it is proposed that the meanings of the concepts of *role* and *caste* be associated with social function and form, respectively. Furthermore, it is suggested that the definition of *caste* should be tied to morphogenesis to give it a mechanistic basis. By a similar argument involving behavioural ontogeny, or ethogenesis, it is shown that attempts to define a categorical concept of function may have little use in social biology.

DEFINITIONS

Stipulative definitions

The concept of *caste* has a long history of use in studies of insect sociality, going back at least as far as 1802 (PEETERS & CROZIER 1988). In the context of insect sociality, caste was originally used to designate the various forms of female found in many insect societies: queens, workers and soldiers. The general correspondence in early socio-ethological studies between the form and function of these physical types led to the inclusion of social function in the sense of the term *caste*. Today it has a number of not entirely compatible definitions incorporating form and function to different degrees.

The original usage has most recently been championed by PEETERS (PEETERS & CROZIER 1988, PEETERS 1990), and is implicit in the distinction between «age polyethism» and «caste polyethism» (WILSON 1971). It is sometimes difficult to apply when variation in *external* morphological traits is continuous (BUSCHINGER 1987,

1990), as is the case in polyphenic ants. However, even in such cases, anatomical traits such as the presence or absence of a spermatheca, have been found that distinguish queens from workers (e.g. BUSCHINGER & WINTER 1978). Broad, continuous variation amongst workers has been described in terms of arbitrary delineated sub-castes (MIRENDA & VINSON 1981).

Another definition, based on function alone, recognizes caste in Hymenoptera as «the forms of females that perform different functions in a colony. They differ from one another at least behaviourally and physiologically, often also in structure, and some of the differences are permanent, not merely due to age» (MICHENER 1974: 32). Such definitions are often imprecise about what is meant by function. They may refer to a broad and general division into reproductive and non-reproductive individuals, or to a finer level of distinction between roles such as foragers, nurses and guards. In clarification of his definition, MICHENER (1974) stated, «In bees the only castes are queen and worker».

A more inclusive definition of castes, based on function, has also been framed: «Any set of colony members, smaller than the total colony population, that specialize on particular tasks for prolonged periods of time» (OSTER & WILSON 1978: 321). Under such a definition, foragers and brood nurses are separate castes, and even larvae of some ants may be regarded as a distinct caste (OSTER & WILSON 1978: 127; HÖLLDOBLER & WILSON 1990: 347). By inference, age polyethism must be a form of caste differentiation. In this light, the phrase «prolonged periods of time» causes operational problems (JAISSON et al. 1988). Essentially, age polyethism causes qualitative differences between patterns of social behaviour measured within time frames of hours, days or weeks. The issue of age groups as castes (HÖLLDOBLER & WILSON 1990) could well be a red herring, since the reported patterns of change in the frequency distributions of behaviours of social insects as they age are probably artifacts of statistical generalization of the behaviour of individuals (JAISSON et al. 1988), which is actually very variable, both qualitatively (CALABI 1988) and quantitatively (MIRENDA & VINSON 1981). Age groups were specifically excluded from MICHENER's (1974: 371) definition.

A third definition combines form and function (e.g. HÖLLDOBLER & WILSON 1990), but this can cause severe operational difficulties (BUSCHINGER 1987, 1990). If one applies both criteria *simultaneously*, there must be a one-to-one relationship between form and function, which is rarely the case. For instance, unmated queen ants may share colony labour with workers (BUSCHINGER & WINTER 1978, TRANIELLO 1978, FRESNEAU 1984), and worker ants may serve the same reproductive function as queens of other conspecific nests (e.g. mated workers of *Rhytidoponera metallica*: WARD 1986). In these and many other examples, individuals of different morphologies fill the same function (BUSCHINGER 1987, 1990). Conversely, in many social bees (MICHENER 1974, 1990), wasps (STRAMBI 1985, 1990) and ants, individuals lacking consistent morpho-anatomical differences fill very varied social functions: individuals functioning as foragers, guards or nurses usually share a common form. In each instance, groups cannot be defined that possess both a unique form and a unique function.

A fourth approach has attempted to surmount this shortcoming by suggesting that «The two positions are conceptually not far apart and can be semantically resolved... The classification should be kept somewhat loose, incorporating either anatomy or roles in a manner that maximizes convenience, precision and clarity of

expression. It must be recognized that anatomy and reproductive role are related across the various ant species not by a one-to-one linkage but by a many-to-many linkage» (HÖLLDOBLER & WILSON 1990: 301).

Perhaps the most vital question, implicit in this final viewpoint, is whether a rigorous distinction between form and function is of any heuristic value to studies of sociality. In particular, we should ask if a *loose* definition can better «*maximize convenience, precision and clarity of expression*».

Operational definitions

The issue of precision raised by HÖLLDOBLER & WILSON (1990: 301) is especially relevant to the quantification of a scientific concept such as *caste*. The four definitions discussed above are stipulative. When technical definitions are also operational, they gain the advantages of making methods of quantification obvious, and of bringing the definitions nearer to having an empirical, perhaps even mechanistic, basis, thus increasing their heuristic value.

Operational definitions aimed at quantifying either form *or* function have been framed informally, without reference to specific stipulative definitions of *caste* (OSTER & WILSON 1978; JAISSEON et al. 1988; VILLET 1989, 1992). The most recent and sophisticated approaches to measuring form have employed bivariate statistics and cartesian techniques (FRANKS & NORRIS 1987, CORRUCINI 1988), while function in social insects has been most effectively explored using a combination of sampling techniques, multivariate classifying algorithms and correspondence analysis (JAISSEON et al. 1988; VILLET 1989, 1992).

An operational definition of caste in terms of form *and* function has been formalized in the idea of a multi-dimensional «allometric space» (OSTER & WILSON 1978: 165), but has never been used in an empirical study. This approach employs a combination of metrical and frequency data to construct the allometric space, and might therefore be considered to be a composite of the above methods. However, the analysis depends on a single (although unspecified) multivariate technique, and thus provides a unified analytical approach to the operational definition of castes.

AREAS OF APPLICATION

Since one of the most important purposes of a scientific definition is to serve the heuristic needs of a discipline, the demands placed on the definition of a technical term are best explored by referring to the fields where it will be used. This means assessing whether there is any need for a distinction between form and function in the definition of *caste*. The aim of this section is to see if the implications of form and function in studies of social insects ever differ enough to warrant defining appropriate terminology to emphasize these differences. No attempt at framing a definition of *caste* is intended in this section, and for this reason, the term is not even used.

Developmental studies, behavioural ecology and social evolution, three major areas of insect socio-biology, provide good arenas for testing the importance of distinguishing between form and function.

Developmental studies

The development of morphological and anatomical form (morphogenesis) and behavioural function (ethogenesis) in individual social insects are both achieved, at least in part, by the actions of hormones (WHEELER 1986, ROBINSON 1987). However, the mechanisms underlying the ontogeny of form and function in social insects are not analogous, let alone homologous. Although both are developmentally plastic and therefore strongly influenced by environment (McDONALD & TOPOFF 1985, WHEELER 1986, CALABI 1988, JAISSEON et al. 1988, GORDON 1989), form retains a smaller measure of plasticity than function (WILSON 1984), especially in the Hymenoptera, where physical differentiation becomes inalterably fixed by the onset of pupation (WHEELER 1986). In the higher termites, the developmental pathways can also reach distinct, terminal (although not adult) states. However, this is not true of morphogenesis in some of the lower termites, where all individuals become reproductive adults (WATSON et al. 1985, NOIROT & PASTEELS 1987). Stress should thus be put on the relative lack of flexibility and reticulation in the pathways of this process compared to ethogenesis, rather than any absolute distinction in determinacy.

The reasons behind the greater indeterminacy of ethogenesis appear to lie in the degree to which the genome is involved in changes to the expression of form and function of individuals. Morphological change involves co-ordinated alterations to the growth, metabolism and communication of whole blocks of cells, which implies changes in genomic regulation of these processes. Short-term changes in behaviour, on the other hand, depend most immediately on modification of the physiological activity of the nervous system, without affecting patterns of intercellular communication. They thus rely on epigenetic mechanisms that need not affect the genome, although they may if they are translated into long-term alterations in behaviour. These differences correspond to the processes of *developmental conversion* and *phenotypic modulation* respectively (SMITH-GILL 1983). Ethogenesis, implying long-term changes in behaviour and social function, may rely on learning, at least in ants (DENEUBOURGH et al. 1987), and could therefore involve both genomic and epigenetic processes.

Because the morphogenetic pathways of social insects tend to remain distinct and discrete once they have diverged, the resulting forms lend themselves naturally to categorical descriptions. Categorization of function is more difficult because of the flexibility of individuals' behaviour. A quantification of the social function of an individual over a period of days is composed of more than merely its behavioural repertoire, or the list of tasks it performed; the relative frequency with which each task was performed also needs to be taken into consideration (OSTER & WILSON 1978). Different individuals combine tasks in different proportions, and these proportions change as they age (GORDON 1989). Because of this, a statistical comparison of the social functions of individuals in the same work-force reveals a spectrum of degrees of similarity in their behaviour. The subdivision of this continuum into groups of individuals showing relatively homogeneous frequencies of each task in their repertoire is largely subjective because most colony members perform most tasks, although with varying frequency (JAISSEON et al. 1988, VILLET 1992). Because of the flexibility of the behaviour of individuals, even under similar conditions, the pattern of functions often varies between colonies, as well as within the same colony censused at different times (RETANA & CERDA 1990).

Morphogenesis is also more conservative than ethogenesis, producing fewer phenotypes: morphological variation seldom reaches the complexity found in behaviour. What underlies this difference? The nervous system is responsible for behaviour and its modification by experience. The general conformation, connectivity, sensitivity and other properties of the neurons making up this system may be genetically prescribed, but the actual connections between neurons are not (ABOITIZ 1988, MICHOD 1989). It is the pattern of connections that ultimately mediates behaviour, and is responsible for the flexibility of behaviour. Perhaps because nervous systems are more sensitive to patterns of interconnections between cells than are other tissue systems, there is more complexity of variation in behaviour than in morphology.

Besides providing clearer insight into the mechanisms of physical and behavioural development, discrimination between form and function can reveal interesting, but otherwise hidden, cases of modified development, such as the absence of the morphogenetic pathway producing queens in some ponerine ants (PEETERS & CROZIER 1988) and the non-homology of some developmental pathways in termites (NOIROT & PASTEELS 1987). In each case, parallels with other species in the social function of individuals obscure the morphogenetic differences between them.

Behavioural ecology

A major theme in the behavioural ecology of social insects is the division of labour, particularly reproduction, amongst members of a colony. Form and function hold overlapping and distinct implications for the ecology of these insects. The differing constraints of the morphogenetic and ethogenetic mechanisms cause qualitative differences between morphology and behaviour as means of maximizing productivity under normal conditions (JEANNE 1986), and as means of accommodating environmental changes (CALABI 1988).

Although form can be highly adapted to particular tasks, this adaptation may happen at the expense of morpho-anatomical adaptation for other tasks. By comparison, behavioural specialization can retain a great deal of flexibility, especially if coupled with relatively unspecialised morphology. JEANNE (1986) has shown that when the risk of death or injury is greater for some tasks than others, it is generally more energetically efficient to divide labour on the basis of age rather than morphology. Only when all risks were very low, and flexibility at less of a premium, was the reverse true.

Flexibility is also essential to meeting environmental changes that happen within the span of an individual's working life. The duration of environmental pressures that change the proportion of individuals performing different jobs can be of the order of hours (WILSON 1984), while pressures that alter the distribution of different physical forms have to last at least the duration of the process of physical differentiation (WHEELER 1986). Thus individuals cannot respond immediately to changing environmental conditions by altering their morphology or anatomy, but can modify their behaviour appropriately (OSTER & WILSON 1978, CALABI 1988). This difference reflects the manner in which colonies as a whole respond to environmental changes (WILSON 1983, 1984; WALKER & STAMPS 1986; JAISSE et al. 1988). Experiments in which morphological groups of worker ants were removed from colonies of *Atta cephalotes*, showed that the losses were not compensated for by differentially rearing individuals of the missing group(s). Rather, the tasks of the missing ants were taken

over by other groups. The ability of individuals to enlarge their behavioural repertoires under such conditions has been termed elasticity (WILSON 1984). As WHEELER (1986) pointed out, elasticity «uncouples morphological and behavioural specialization», diminishing their inter-dependence.

Finally, the reproductive interests of queens and workers are usually very different, since the latter are often sterile. Even when the external morphologies of the two intergrade, anatomical differences may exist in their reproductive systems (BUSCHINGER & WINTER 1978) that are critical to their reproductive potential, and result from different morphogenetic histories. Distinguishing between the two morphogenetic pathways is critical to, for instance, assessing the occurrence and significance of the polymorphism found in queens of some myrmicine ants (BUSCHINGER 1978, HEINZE 1989). Where a distinction between form and function allowed the identification of hidden morphogenetic pathways in developmental studies, here it allows the assessment of social function when it is obscured by morphology.

Social evolution

Except in many termites, morphology and behaviour have not generally evolved in parallel in insect societies, indicating that they have little evolutionary equivalence. Morphological diversification has never arisen in a lineage as an evolutionary novelty before the advent of behavioural division of labour (WILSON 1971, NOIROT & PASTEELS 1987). Perhaps it can arise only in the already established context of behavioural differentiation (JEANNE 1986).

Morphological change, because of its genomic component, is open to direct evolutionary selection, while behaviour, because of the involvement of epigenetic, as well as genetic, mechanisms is not as open (SMITH-GILL 1983). For instance, although the properties of individual neurons may be genetically prescribed and open to selection, the inter-connections that actually occur are under epigenetic regulation (MICHOD 1989). While natural selection does not directly affect behaviour, it helps to re-shape variation in behaviour. Behavioural variation is rich relative to morpho-anatomical variation, providing a greater source of evolutionary novelty. If morphology does constrain behaviour, as shown in *Pheidole* (WILSON 1984) and implied in termites (NOIROT & PASTEELS 1987), the evolutionary relationship between the two might be hierarchical rather than reciprocal. If this is the case, there may be evolutionary advantages to avoiding morpho-anatomical specialization. The differences between morphology and behaviour lead to the expectation that colony fitness could be increased faster, at least in the short term, by changes in behaviour (CALABI 1988).

Evolutionary selection can operate on social insects at two levels (OWEN 1989). Selection at the level of the colony operates on both form (the frequency distribution of morpho-anatomical classes) and function (the frequency distribution of behavioural classes). Selection at the level of the individual can also operate directly on morphology, at least in the Hymenoptera and the soldiers of termites, where each individual is committed to a single form. However, the behavioural flexibility of individuals shields (but does not remove) them from individual selection of functional traits. There are therefore several reasons for treating form and function as separate concepts in evolutionary socio-biology.

TERMS AND DEFINITIONS

The above discussion has shown that a more sophisticated insight into processes affecting social organization in insects can be gained by explicitly distinguishing the form of colony members from their function, rather than by treating the two as implicitly equivalent concepts. Furthermore, this position is implicit in the recognition of the many-to-many linkage between these two phenomena. While a loose definition may be convenient, it hampers clear, precise thinking about the relationship between function and form of social insects, and does not reflect the depth of current knowledge of insect sociality.

Because sociality has many independent evolutionary origins in the insects, neither form nor function can be a phylogenetically homologous social phenomenon. However, there are important mechanistic homologies structuring both that underly these multiple and separate origins (since they all arose within the same context of insect development and neurobiology), so that the concept of *caste* remains unified and has an overarching usefulness even when discussing phylogenetically unrelated insect societies. This means there is justification for seeking separate terms for discussing form and function. What terms are available, how are they understood, and which should be associated with *caste*?

The oldest usage of *caste*, to connote form alone, can be paired with a newer term for the social function an individual performs: its *role* (OSTER & WILSON 1978, HÖLLDOBLER & WILSON 1990, VILLET 1992). Because of its long history of implicit use, the morphological concept of *caste* is associated with numerous adjectives and technical nouns that designate form (e.g. WILSON 1953), and requires only a more rigorous application of the descriptive terms to specify an individual's function or role. Thus, this approach would specify three castes (queen, worker and soldier), while roles are easily provided with informal descriptive names *ad hoc* (e.g. forager, nurse, reproductive). A plethora of terms can be gathered from studies of wasps and bees, where they are used to describe the functions of females during various stages of the growth and senescence of a colony (EICKWORT & KUKUK 1987, modified by MICHENER 1990).

Conversely, MICHENER (1974) and BUSCHINGER (1987, 1990) proposed a newer usage of *caste* to denote only function, emphasizing a criterion of reproduction. BUSCHINGER (1987) explicitly synonymised *caste* with role. Physiological and taxonomic studies could then use a new term, such as *morph*, to denote physical form, in uniformity with studies of other orders of insects (e.g. NIJHOUT & WHEELER 1982). A new approach to terminology is needed if *caste* is to connote function rigorously (BUSCHINGER 1978). In particular, one would have to specify numerous new terms for castes *ad hoc* to meet the needs of studies of labour, because of the flexible way in which individuals combine tasks into roles. Occasionally, form would need to be qualified by appropriate adjectives (e.g. gynomorphic, interomorph, ergatomorphic, major: BUSCHINGER 1987) when a species is polymorphic.

The definition of *caste* based on function alone can be rejected for several reasons. The concept of *caste* is explicitly categorical (OSTER & WILSON 1978, NOIROT & PASTEELS 1987, PEETERS & CROZIER 1988, HÖLLDOBLER & WILSON 1990), and this is where it gains most of its heuristic importance. The definition of *caste* by function is often operationally imprecise because of the subjectivity inherent in subdividing the continuum of social functions that arises when individual insects perform tasks at

different frequencies (JAISSEON et al. 1988, VILLET 1992). For this reason, this formulation also fails to preserve the connotation of categorical classification that gives *caste* some of its scientific usefulness. When the operational difficulties of defining categories of behaviour are viewed with a functional or pluralistic definition of caste in mind, one may soon reject the usefulness of the concept of *caste*, and call for its replacement by a new conceptual framework entirely (GORDON 1989). Finally, the changes that a functional definition necessitates in the established terminology associated with *caste* (BUSCHINGER 1987) can lead to confusion in the interpretation of the existing literature on this subject. A morpho-anatomical definition lacks these disadvantages.

If these arguments are accepted, what would constitute a caste? An ideal definition of *caste* should be mechanistic and operational, rather than merely stipulative, and should have heuristic value.

It is becoming possible to root any definition of *caste* in an understanding of the mechanisms underlying the phenomena being described, i.e. in their developmental processes. Because morphology and anatomy are the products of ontogenetic processes, a mechanistic definition of caste in terms of form implies a distinct morphogenetic pathway underlying each caste. *Caste* may be defined as the subdivision of a colony of social insects into groups characterized by a shared morphogenetic pathway that has diverged irreversibly from that of other such groups in the colony. The most obvious types of caste would be queen, worker and perhaps soldier, if the latter is distinct and discrete, as in termites (WATSON et al. 1985, NOIROT 1990) and some ants (WILSON 1953). The criterion of ontogenetic divergence restricts the application of this definition to the differentiated portions of the morphogenetic process, and therefore excludes the larvae of termites and Hymenoptera from being defined as castes. The criterion of irreversibility should not be confused with one of immutability, since distinct morphogenetic pathways may span more than one instar, and thus more than one morphology, in termites (WATSON et al. 1985, NOIROT & PASTEELS 1987, NOIROT 1990). Neither should *caste* carry connotations of adulthood, because termite soldiers retain their prothoracic glands, and are thus not adults, even though they are irreversibly differentiated from other morphogenetic pathways (NOIROT & PASTEELS 1987).

Operationally, the products of divergent ontogenies are most distinct at their endpoint. Once it has been established by developmental studies that more than one morphogenetic pathway is present, there are a variety of morphometric techniques appropriate for characterizing the castes by their products (e.g. OSTER & WILSON 1978, FRANKS & NORRIS 1987, JAISSEON et al. 1988, CORRUCINI 1988). In cases of morphogenetic divergence that span more than one instar, each morphology can be recognized as an instar within a caste. If morphology spans a large continuum within a single instar, and if there is any heuristic need to do so, the concept of a *sub-caste* could be used for parts of the spectrum that can be defined only subjectively (cf. MIRENDA & VINSON 1981). However, there are indications that what are currently taken as sub-castes in certain species could be the products of distinct morphogenetic pathways or series of morphogenetic events (*sensu* ALBERCH et al. 1979) that produce overlapping character distributions. If this is true, the result of each pathway should have a characteristic, distinct mean and standard deviation associated with it (OSTER & WILSON 1978). In species where the distribution of worker sizes is distinctly bimodal, this may be the case, and would imply separate castes. Where distinct

developmental events, such as passing a developmental threshold, are absent, size variation arises solely from differences in the amount of food received during the larval stages. The extremes of such size distributions would not be regarded as separate castes.

What are the practical and heuristic implications of applying the morpho-anatomical concept of *caste* rigorously? Some species of ants (e.g. some ponerines: VILLET Ms01), social bees (e.g. many halictids: MICHENER 1990) and social wasps (e.g. some stenogastrines and polistines: STRAMBI 1985, 1990) in which the females filling different roles are morphogenetically indistinguishable would be without castes. Similarly, in some primitive termites, there is only one distinct morphogenetic pathway, since all of the individuals performing social tasks later become reproductives (NOIROT & PASTEELS 1987, NOIROT 1990). These species would also lack castes. The division of labour in species where absence of caste is primary, as in many bees, wasps and termites, is achieved solely through the evolution of behaviour, giving these societies a special place in the study of social polyethism and polymorphism that cannot be filled by secondarily casteless societies such as those of queenless ants.

The heuristic advantages of adopting separate concepts are also clear where a morphogenetic pathway has been lost, since it is of developmental, ergonomic and evolutionary interest to identify which is missing. In parasitic ants and hornets, loss of the worker pathway has ecological significance (LE MOLI & MORI 1987); in some ants the queen pathway has been lost, apparently by accident (VILLET Ms01).

This approach to defining *caste* provides a perspective that is in need of empirical testing for its heuristic usefulness. It is hoped that it will encourage research into behavioural and morpho-anatomical ontogeny and the relationship between form and function in social insects, and that it will be re-evaluated if substantial isomorphisms are discovered.

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