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Review

Ergatoid queens and intercastes in ants: two distinct adult forms which look morphologically intermediate between workers and winged queens

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Summary

The term "ergatogyne" is used in ants to describe permanently-wingless female adults which are "morphologically intermediate" between workers and winged queens. This definition is ambiguous because there are two distinct categories of "ergatogynes": ergatoid queens and intercastes. Both have an external appearance (ocelli and alitrunk structure) which combines traditional queen and worker characters, and thus can be confused if they both function as reproductives – however intercastes in most species cannot reproduce.

Ergatoid queens have replaced winged queens in a substantial number of species. They are sometimes externally similar to conspecific workers, especially in various ponerine species which exhibit limited size dimorphism between castes. Ergatoid queens retain the specialized attributes of a reproductive caste, including larger ovaries, and they are always the functional egg-layers in a colony. In contrast, conspecific intercastes represent various graded stages in a series connecting workers and winged queens, and they occur together with the queens. These hybrid phenotypes result from deviations from the normal pattern of caste differentiation during larval development. Intercastes generally lack a spermatheca and have no reproductive function; however they can mate in a few leptothoracine ants, and then reproduce instead of winged queens in a proportion of colonies.

Introduction

The social organization of ant colonies is intricately linked with the existence of two physical castes. Queens and workers differ both in internal morphology (wing muscles, reproductive organs) and in external appearance (queens are generally bigger, and eclose with wings which are lost after copulation – wings are associated with a modified thorax having flight sclerites). This dimorphism often specifies the separation of roles in a colony, and only the queens reproduce sexually. However, there exist two general exceptions to this pattern of division of labour.

Firstly, variants to the typical queen and worker forms occur in a substantial number of species. These individuals have an external appearance which combines traditional queen and worker traits – in particular they have ocelli, and an enlarged alitrunk characterized by simplified flight sclerites, even though they are wingless. They have often been referred to as "ergatogynes" ("any form morphologically intermediate between the worker and the queen", Wilson, 1971:463), although several other terms have also been used. "Ergatogynes" mate and reproduce in various species, but not in others. Secondly, the queen caste has disappeared in a few ants. In some species of the subfamily Ponerinae, inseminated workers ("gamergates") reproduce instead (Peeters, 1987; Peeters and Higashi, 1989), while in the Myrmicinae *Pristomyrmex pungens*, unmated workers are able to lay haploid and diploid eggs (Itow et al., 1984; Tsuji, 1988).

In this paper I argue that the term "ergatogyne" is confusing and lacks precision in that it describes two different types of adult females: (1) *ergatoid queens*, members of a persistently-wingless reproductive caste, which have evolved from winged queens; and (2) *intercastes*, conspecific series of individuals with hybrid phenotypes, i.e. exhibiting the uncoordinated expression of various queen and worker characters (ocelli, alitrunk structure, and reproductive organs). Only in some leptothoracine ants do intercastes assume a reproductive role. The formal distinction which I advocate between ergatoid queens and intercastes was foreglimpsed by Wilson (1971:138), who differentiated between species in which ergatogynes replace the winged queens entirely and are not connected to the worker caste by a graded series, and species in which winged queens persist and ergatogynes form a graded series between them and the typical workers. While the ergatoid condition is a permanent evolutionary modification of the ancestral queen morphology, intercastes are a developmental peculiarity and are often produced erratically.

Little is known about the reproductive biology of ergatoid queens in the subfamily Ponerinae, and I present new data about several species. Throughout this text, "queen", "worker" and "caste" are used strictly in a morphological sense, not in a functional sense (Peeters and Crozier, 1988).

Materials

Nests of the following ponerine species with ergatoid queens were collected in various locations (Tab. 1) in South Africa (1982–1985) and Australia (1986–1987). Care was taken to collect entire colonies. Ergatoid queens and a sample of the workers in each species were dissected in order to examine ovaries and spermathecae. Voucher specimens have been deposited in the British Museum (Natural History), and the Australian National Insect Collection, respectively.

Ergatoid queens

Literature review

Wingless queens occur instead of normal winged queens in a substantial number of ant species (Wheeler, 1910). The evolutionary loss of wings and flight muscles has been accompanied by various degrees of simplification of the flight sclerites and

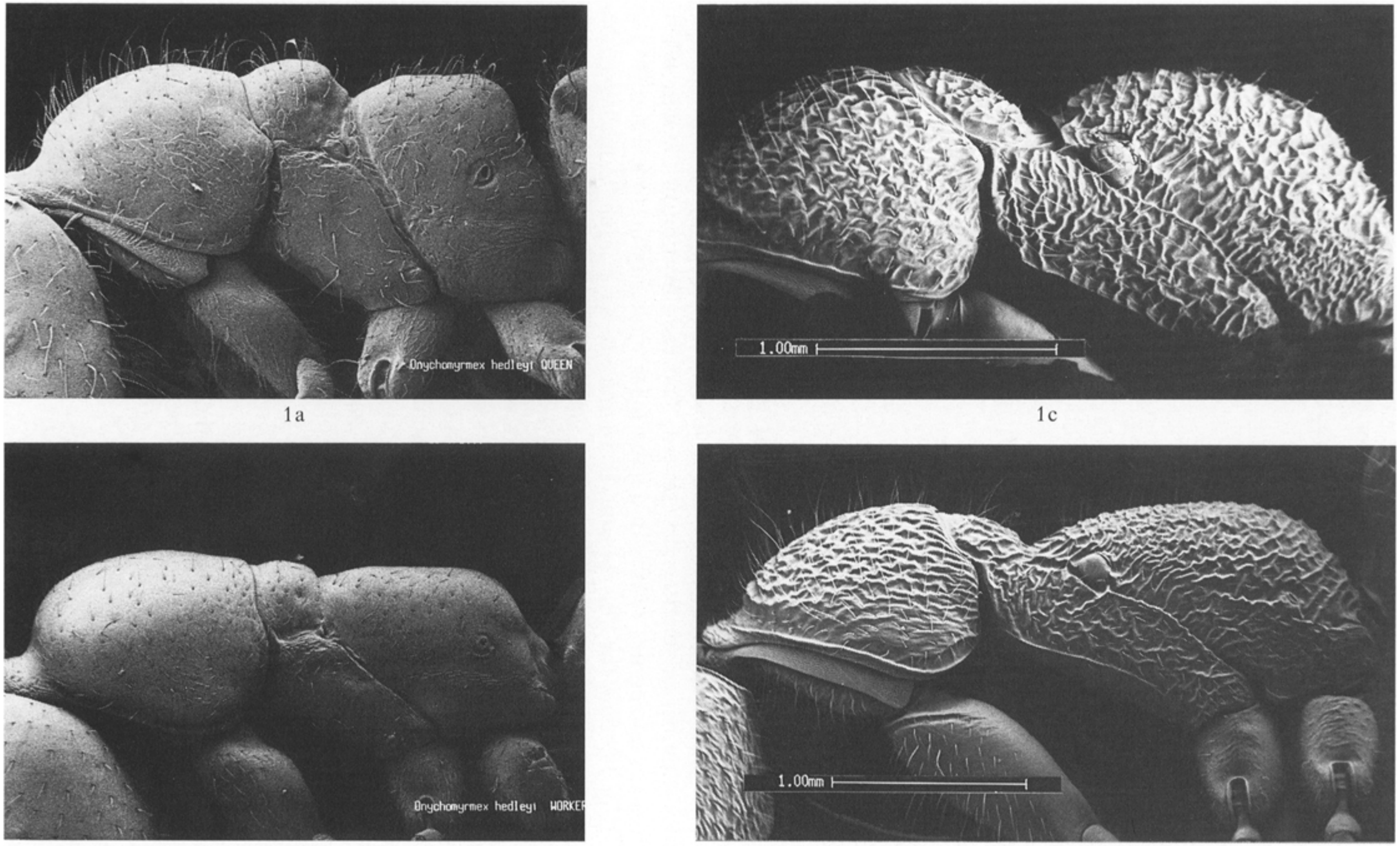
Table 1. Details of the localities (in South Africa and Australia) where colonies of ponerine and cerapachyine ants with ergatoid queens were collected. Abbreviations are RSA: South Africa; FNQ: far north Queensland; NSW: New South Wales

Locality	species	number of colonies	description of nesting site
Knysna, southern Cape, RSA	*Leptogenys nitida*	2	surface layers of soil
Hoedspruit, eastern Transvaal, RSA	*Megaponera foetens*	2	20–30 cm deep in soil
Yungaburra, Atherton Tableland, FNQ	*Onychomyrmex hedleyi*	4	bivouac under a stone
	Leptogenys mjobergi	3	surface soil under stone
	L. longensis	4	in rotting fallen log
Lake Eacham, Atherton Tableland, FNQ	*Heteroponera relicta*	1	in rotting fallen log
Kakadu National Park, Northern Territory	*Cerapachys* c.f. *heros*	1	shallow nest in soil
	Leptogenys exigua	1	50 cm deep in soil
Blue Mountains, NSW	*Sphinctomyrmex* c.f. *steinheili*	3	under a stone

thoracic sutures. Bolton (1986) showed that the wingless queens which occur in various species of the *Monomorium salomonis*-group exhibit varying stages in a morphoclinal reduction in the alitrunk sclerites, both in size of individual components and in number of sclerites represented. This modification in the alitrunk of wingless queens sometimes results in a superficial similarity in appearance to the workers (Fig. 1), and for this reason these queens have been termed *ergatoid* ("worker-like").

Ergatoid queens occur widely in the Ponerinae (12 genera in all four tribes), and also in other subfamilies (Tab. 2). Sometimes they occur throughout a genus, but often they are found in only some of the species belonging to a genus. Wingless queens occur in every species of all army ant subfamilies, and they have traditionally been termed *dichthadiiform*. These never resemble the workers because of several characteristics, including a huge gaster and expanded postpetiole (Wilson, 1971:139). The extreme enlargement of the gaster seen in dichthadiiform queens seems associated with the cyclical production of large numbers of eggs, a prerequisite for a legionary mode of life.

In the Ponerinae wingless queens look most like the workers, because a very limited difference in stature between the castes is a characteristic of this phylogenetically-primitive subfamily. Nevertheless distinct differences in external appearance remain (Fig. 1), e.g. queens have ocelli (although often reduced or vestigial), their alitrunk exhibits vestiges of the metanotal groove, their mesonotum is larger than in workers, and their gaster is bulkier (e.g. Bolton, 1974). Caste differences are most dramatic in the ponerine genera *Onychomyrmex* and *Simopelta*, in which wingless queens approximate the dichthadiiform condition (Wilson, 1958b; Gotwald and Brown, 1966).



1a 1c

1b 1d

1b 1d

Figure 1. Scanning electron micrographs (lateral view) of the alitrunks of ergatoid queens and workers in two ponerine ants: *Onychomyrmex hedleyi* (a) and (b), *Leptogenys longensis* (c) and (d). In these species the absence of wings is accompanied by an extreme reduction of the flight sclerites, and thus the alitrunks of both castes are very similar

Table 2. List of ant genera in which ergatoid queens (as defined in this paper) have been reported

Genus		References
Subfamily Ponerinae		
Onychomyrmex	all species *	Brown, 1960:178
Discothyrea	some species	Brown, 1958 a:251
Gnamptogenys	some species	Brown, 1958 a:225
Heteroponera	most species	Brown, 1958 a:195
Proceratium	some species	Brown, 1958 a:245
Platythyrea	*conradti*	B. Bolton, pers. comm.
Hypoponera	*eduardi*	Le Masne, 1956
Leptogenys	most species	e.g. Bolton, 1975
Megaponera	*foetens*	Arnold, 1915:48
Plectroctena	4/11 species	Bolton, 1974
Prionogenys	*rouxi*	Wilson, 1958 a
Simopelta	*oculata* *	Gotwald and Brown, 1966
Subfamily Cerapachyinae (following Bolton, 1990)		
Cerapachys	some species	Brown, 1975:19
Sphinctomyrmex	some species	Brown, 1975:31
Acanthostichus	all species *	Brown, 1975:40
Subfamilies Dorylinae, Ecitoninae, Leptanillinae		
all genera	all species *	Gotwald, 1982
Subfamily Myrmicinae		
Calyptomyrmex	2/6 African species	Bolton, 1981 a
Megalomyrmex	*leoninus*-group +	Brandão, 1990
Monomorium	several species-groups	Bolton, 1987; Dubois, 1986
Octostruma	1–2 species	Brown and Kempf, 1960
Ocymyrmex	all species	Bolton, 1981 b
Pristomyrmex	*pungens* #	Itow et al. 1984
Stereomyrmex	*horni*	B. Bolton, pers. comm.
Subfamily Myrmeciinae		
Myrmecia	some species	Clark, 1951
Subfamily Dolichoderinae		
Leptomyrmex	all species	Wheeler, 1934
Subfamily Formicinae		
Proformica	one species (indet.)	D. Agosti, pers. comm.

* dichthadiiform condition
\+ these ergatoid queens were described incorrectly as "gamergates"
\# not functional (see text)

In the Myrmicinae, ergatoid queens are often substantially larger than workers and, although the alitrunk exhibits reduced complexity, they cannot be mistaken (e.g. *Pristomyrmex, Calyptomyrmex, Stereomyrmex, Monomorium*). However, the ergatoid queens of *Ocymyrmex* exhibit a remarkable resemblance to the workers, although the former remain characterized by specialized morphology (Bolton, 1981 b; Bolton and Marsh, 1989). Thus in *O. foreli*, ergatoids have 30–34 ovarioles, while workers have two ovarioles and no functional spermatheca (Forder and Marsh, 1989). The reproductive structure of myrmicine species with ergatoid queens is known only in *O. foreli*. While ergatoids form a substantial proportion (4–20%) of the adult population of each colony, only one inseminated ergatoid is found per colony, and unmated ergatoids take part in non-reproductive activities (Forder and Marsh, 1989). In contrast, 5–10 inseminated ergatoids have been found in two colonies of *Monomorium creticum* (A. Buschinger, pers. comm.). In *Pristomyrmex pungens*, ergatoid queens were shown not to be functional, and reproduction is performed exclusively by unmated workers (Itow et al., 1984).

In *Myrmecia*, ergatoid queens occur in many species, and brachypterous queens (with wings developed to only a third or less of normal length) are found in some others (Clark, 1951). Unfortunately little is known about the biology of queen modification in this genus (see Haskins and Haskins, 1955).

There is clear comparative evidence that ergatoid queens have evolved from the ancestral winged queens. In many genera winged queens have been retained in certain species while ergatoid queens occur in the others. The transition between the two queen forms is nicely illustrated in *Leptogenys*. Winged queens occur in *L. langi*, while ergatoid queens occur in all other species – the latter have alitrunks which are practically indistinguishable from the workers', except in *L. ergatogyna* where the wingless queens have an alitrunk with flight sclerites almost like that of the normal queens in *L. langi* (Wheeler, 1923). In *Hypoponera* (= *Ponera*) *eduardi*, both winged queens and ergatoid queens occur in the same populations, although not in the same colonies (Le Masne, 1956) (it was initially reported that "major workers" mated and had active ovaries, but these are clearly ergatoid queens, see Brown, 1958b:23). *H. eduardi, H. opacior* (Ward, pers. comm.), and *Proceratium* (Brown, 1958a:245) are the only species in which winged and ergatoid queens have been found conspecifically; in other ants studied, ergatoid queens are the exclusive sexual forms whenever they occur.

Results

As part of this study, the ergatoid queens of nine species were dissected and their reproductive organs examined (Tab. 3). With the exception of the polygynous *Sphinctomyrmex steinheili*, only one mated queen was found in each of 18 nests that were excavated. In some species, ergatoid queens have more ovarioles than the workers, while in others there is no difference in the respective numbers of ovarioles, although the queen ovarioles are considerably longer (even when reproductively inactive). This pattern is similar to that in ponerine species with winged queens, i.e.

Table 3. Structural differences between the ovaries of ergatoid queens and workers in various ponerine and cerapachyine species. The number of workers found in individual nests is also indicated. Only one ergatoid queen was found in each nest, except in *Sphinctomyrmex steinheili* (see Buschinger, Peeters and Crozier, 1989)

Species [number of queens and workers dissected]	no. of ovarioles per ovary		colony size
	queen	worker	
Onychomyrmex hedleyi [3, 6]	3	2–3	543 ± 184 ($N = 4$)
Cerapachys c.f. *heros* [1, 2]	2	1	15?
Sphinctomyrmex c.f. *steinheili* [20, 17]	2–5	1	400, 201, 89
Heteroponera relicta [1, 5]	4	1	73
Leptogenys mjobergi [2, 6]	3	2–3	44, 22, 28
L. longensis [2, 2]	3	3	37 ± 13 ($N = 4$)
L. exigua [1, 2]	4	4	232
L. nitida [2, 7]	13–14	1–2	245, 184
Megaponera foetens [1, 10]	32	12–15*	2029, 632

* this species has a polymorphic worker caste, and this refers to major workers

queens do not always have more ovarioles than workers (Peeters, 1987). There is no indication that the loss of wings has been accompanied by a reduction in reproductive potential of queens. In fact, the ergatoid queens in some species are exceptionally fecund, e.g. an ergatoid of *Megaponera foetens* laid 32,8 eggs/day in the laboratory (over 6 days) – for comparison, a more typical egg-laying rate is that of *Leptogenys exigua* (4,7 eggs/day over 8 days). While several species with ergatoid queens have colonies with less than 100 workers, this is a general characteristic of the Ponerinae, not of ergatoids. Indeed, some species with winged queens also have small colonies, while monogynous colonies of some species with ergatoid queens can grow to a large size (e.g. *Onychomyrmex* and *Megaponera*; Tab. 3). Indeed, the largest colonies recorded in this subfamily are those of *Leptogenys* sp. 1 (c. f. *mutabilis*), which are monogynous and reach an average size of 46750 workers (Maschwitz et al., 1989).

Discussion

Although the term "ergatoid" was used as early as Holliday (1903) to describe "worker-like" reproductives, its use should be restricted to describing permanently wingless queens. It must be emphasized that the occasional resemblance of wingless queens to workers is in external appearance only. In other aspects of their biology, ergatoid queens clearly belong to a morphologically-specialized reproductive caste. This is most evident in the wingless queens of army ants, which are among the most fecund of all ant queens (Gotwald, 1982). Thus the description of ergatoid queen as "a stabilized intermediate between normal queen and worker" (Haskins and Haskins, 1965) is misleading because it implies loss in egg-laying specialization. This idea seems to have stemmed from the study of ergatoid queens in ponerine ants such as some species of *Leptogenys* where they are not easily distinguished from workers.

There is considerable variation in the degree to which the alitrunk of ergatoid queens has been simplified. Once there is no longer an adaptive advantage to aerial dispersal or energy storage in the form of flight muscles, the functional constraints affecting the structure of the thorax change, and fusion of sclerites can occur. Nonetheless, the alitrunk of ergatoid queens has never become identical to the workers' (except in *Ocymyrmex*; Bolton, 1981 b), which probably is a reflection of their evolutionary history. Furthermore, since the ergatoid modification has evolved repeatedly in independent lineages (i.e. in different subfamilies, and in different tribes within the Ponerinae), we should not expect that the concomitant modifications in the alitrunk would converge to the same pattern. In *Monomorium rufulum* (Bolton, 1986) and *Leptogenys ergatogyna* (Wheeler, 1923), queens are wingless and yet show no reduction of the typical alate alitrunk. There are also species (e.g. *Myrmecia, Nothomyrmecia*) in which queens are either brachypterous (with short non-functional wings and a normal alitrunk with flight muscles) or fully-winged (Clark, 1951; Hölldobler and Taylor, 1983). The adaptiveness of wing loss in ant queens is not well understood (but see Bolton, 1986).

Intercastes

Literature review

In ants and other highly-eusocial insects, female larvae develop according to either of two developmental programs, which produce morphologically-discrete adult forms (queens or workers). There are no intermediates in the vast majority of species, irrespective of whether queens are winged or ergatoid. However several species are known (Tab. 4) in which there exists in addition a series of female forms with various combinations of queen and worker characters. These *intercastes* are usually rare and without functional significance, but in a few leptothoracine ants they are produced regularly, and they mate and reproduce.

Various detailed studies have focused on the characteristics of intercastes (Plateaux, 1970; Buschinger and Winter, 1975; Francoeur et al. 1985). They are not winged although their alitrunk is distinguished by simplified flight sclerites. Ocelli number, thoracic structure, body size, number of ovarioles and size of spermatheca vary continuously between the queen and worker castes. While distinct allometric relationships specify the development of these characters in queens and workers, it is not so in intercastes (e.g. Francoeur et al. 1985). This difference was clearly demonstrated in *Leptothorax nylanderi*, where the dimensions of head, thorax and gaster of intercastes increase independently of one another (Plateaux, 1970). Similarly, the growth of ovaries and spermatheca are not correlated with external morphological traits, e.g. an intercaste of *L. nylanderi* with an almost queen-like thorax and large abnormal wings, only had two ovarioles (queen have 8 ovarioles, workers have 2) and a spermatheca one third the size of a queen's. Brian (1979) described the conditions under which he was able to produce intercastes in *Myrmica ruginodis* (= *rubra*), by artificial manipulation (e.g. starving queen-presumptive larvae at a

Table 4. List of ant species in which intercastes have been described. Winged queens exist in all these species. A question mark indicated a lack of data

Species	does intercaste have a spermatheca?	References
Harpagoxenus sublaevis	yes	Buschinger and Winter, 1975
H. americanus	no	Buschinger and Alloway, 1977
H. canadensis	no	Buschinger and Alloway, 1978
Formicoxenus (6 species)	yes	Francoeur et al. 1985
Leptothorax nylanderi	sometimes	Plateaux, 1970
L. retractus	?	Francoeur, 1986
L. sphagnicolus	yes	Francoeur, 1986
L. sp. A (cf. *muscorum*)	yes	Heinze and Buschinger, 1987
Monomorium pharaonis	?	Hall and Smith, 1953
M. rubriceps cinctum	?	Wheeler, 1917:113
Pogonomyrmex californicus	?	Tulloch, 1930
Myrmica ruginodis	?	Brian, 1955
Messor structor	?	Plateaux, 1970:409
Camponotus cruentatus	?	Plateaux, 1970:409
Polyergus rufescens	no	Stitz, 1939; Buschinger, 1978
Formica nigricans (= *rufa pratensis*)	?	Bier, 1954
Plagiolepis (= *Aporomyrmex*) *ampeloni*	?	Faber, 1969
P. pygmaea	yes	Passera, 1969
Technomyrmex sp.	yes	Terron, 1972

particular developmental stage), and naturally (e.g. diapause larvae in spring that are below the average queen size – a nutritional switch then occurs, the pattern of development changes, and wing and ovary growth stop while the growth of other body parts is enhanced).

In most species intercastes lack a functional spermatheca (Tab. 4) and thus cannot mate. In *Leptothorax nylanderi*, some intercastes have a spermatheca but were never found to be mated (Plateaux, 1970). However in a few social parasites, intercastes are reproductively-active and can replace the queen caste (e.g. *Harpagoxenus sublaevis* and 5 species of *Formicoxenus*; Buschinger and Winter, 1978; Francoeur et al. 1985; referred to as "intermorphs"). In *H. sublaevis*, intercastes always have a spermatheca, and both workers and intercastes may have as many ovarioles as the queens. Queens are extremely rare, and mated intercastes reproduce instead (Buschinger and Winter, 1975, 1978). In *Formicoxenus*, intercastes generally have a normal spermatheca and 6 ovarioles (as do queens; workers have 2 ovarioles). Very few queens are produced (1,6–4,1 % of nest population). A large proportion of dealate queens and intercastes are mated. Several mated individuals can be present in one nest, but only one is fertile (Buschinger, 1979; Buschinger and Winter, 1976; Buschinger et al. 1980). In *F. provancheri* and *F. quebecensis*, some workers also have a spermatheca, and they can become mated and reproduce (Francoeur et al., 1985).

Intercastes with a reproductive function are not restricted to social parasites. In *Leptothorax* sp. A, intercastes always have a spermatheca and have as many ovarioles as the queens. Colonies are always monogynous, and the majority have a fertile intercaste instead of a queen (Heinze and Buschinger, 1987). Mated fertile intercastes also occur in *Technomyrmex* sp., in which winged queens are produced irregularly (Terron, 1972). Although the former were originally referred to as "major workers", it seems that they are in fact intercastes. They have a thorax very similar to the workers', and 14–18 ovarioles (workers have 4).

Discussion

Comparative data from the leptothoracines indicate the homology of the reproductive intercastes in some ants and the sterile intercastes in others. While intercastes replace the queens in many colonies of *Harpagoxenus sublaevis*, intercastes are non-functional in *H. canadensis* and *H. americanus*. They lack a spermatheca and thus cannot mate (Buschinger and Alloway, 1977, 1978), while queens are produced in large numbers and are the only functional egg-layers. A minority of workers and intercastes lay unfertilized eggs (Buschinger and Alloway, 1978). It seems evident that in species in which intercastes are morphologically very similar to conspecific queens, they are able to replace the queens since they have comparable egg-laying potentials. Thus in *Formicoxenus, Leptothorax* sp. A, and *Harpagoxenus sublaevis,* workers, intercastes and queens all may have identical ovaries (although workers normally lack a spermatheca). Another prerequisite for the replacement of winged queens is a modified mating pattern, e.g. sexual calling near natal nests, and mating with foreign males near or inside these nests. Finally, in species having reproductive intercastes, the latter are produced in large numbers (e.g. in *Formicoxenus,* 20–50% of nest population). This seems the result of directional selection, and is concomitant with a decrease in the numbers of virgin queens produced. More usually, intercastes are produced erratically and in small numbers (0,5–5% of worker population in *Leptothorax nylanderi;* Plateaux, 1970).

It is possible for the reproductive intercastes in various leptothoracine ants to be mistaken for ergatoid queens. In addition to exhibiting higher egg-laying rates than workers, and being able to mate, they also can inhibit nestmates (mated and unmated) from laying eggs (Buschinger, 1979; Buschinger and Winter, 1978; Buschinger et al. 1980; Heinze and Buschinger, 1987). Nonetheless several biological differences exist between intercastes and ergatoid queens (Tab. 5), and they need not be confused (even when both forms exist in different species within the same genus, e.g. *Monomorium;* Hall and Smith, 1953; Bolton, 1986). Most importantly, (i) ergatoid queens have replaced winged queens, while intercastes occur together with winged queens (with the sole exception of the Swedish populations of *Harpagoxenus sublaevis*); (ii) ergatoid queens are always the functional reproductives in the species where they occur, but this is not the case with intercastes; (iii) conspecific ergatoid queens do not vary morphologically, while intercastes exhibit considerable morphological variability within each colony. In the few species in which intercastes reproduce, these exhibit a range of alitrunk development.

The Swedish populations of *H. sublaevis* are exceptional, because winged queens have never been found and have been completely replaced by intercastes. Further-

Table 5. Outline of various differences between the biology of ergatoid queens and intercastes

Ergatoid queens	Intercastes
occur instead of winged queens *	produced as well as winged queens
morphological characteristics are fixed in each species, i.e. conspecific ergatoids are identical	a graded series of morphological forms is found in each species, i.e. conspecific intercastes are not all alike
clear and abrupt difference in morphology between queens and workers	continuum between winged queens and workers
alitrunk with simplified flight sclerites; ocelli often distinct; ovaries remain specialized	different degrees of simplification of flight sclerites and ocelli; ovaries are often intermediate between queens and workers #
spermatheca always occurs	spermatheca occurs in a few species
always the functional egg-layer in colonies $	functional egg-layers in a few species; then replace queens in some colonies but not others

* *Ponera eduardi* is a well-documented exception (Le Masne, 1956)
\# in *Formicoxenus* and *Harpagoxenus sublaevis*, all adults may have the same number of ovarioles
$ except in *Pristomyrmex pungens*, in which workers reproduce instead

more, the intercastes that occur are all identical (Bourke, 1987). If these ants were considered in isolation, we would place their reproductive forms into the ergatoid queen category, because they fit the characteristics listed in Table 5. A different perspective is gained however once we consider the German populations of *H. sublaevis;* here both winged queens and intercastes are found, and the intercastes consist of a graded series of intermediates (Buschinger and Winter, 1975). Thus it seems that the polymorphism in *H. sublaevis* has been modified and stabilized in the Swedish populations, where both worker-like intercastes and winged queens have been eliminated.

A holistic understanding of the phenomenon of intercaste occurrence is possible when we consider the pattern of caste differentiation during larval development. In her review of caste determination in social hymenopterans, Wheeler (1986) pointed out that at various stages during development, the nutritional history of a larva can determine the endocrine signals which co-ordinate subsequent patterns of development (= conditional nutritional switch). In intercastes, the expression of various queen traits during the development of worker-presumptive larvae (or vice-versa) may be the consequence of idiosyncratic differences in tissue sensitivity when hormone levels are near threshold. In contrast, absence of wings and associated musculature in ergatoid queens is a normal developmental response to the endocrinological environment, and other aspects of caste differentiation are unaffected.

The timing of developmental switches varies considerably among ants. The differing mechanisms of queen control over offspring development change the characteristics of morphological specialization in adults (Wheeler, 1986), and thus there may be more developmental plasticity during larval differentiation in some subfamilies. This would explain the phylogenetic occurrence of intercastes, which are absent (although they may have been overlooked) in the Ponerinae, Myrmeciinae and Dorylinae. In many species intercastes are extremely rare and probably develop accidentally. In leptothoracine species where queens are rare and intercastes are produced in large numbers, selection may have lowered the threshold (tissue sensitivity to JH?) for the expression of some queen characters.

Terminology

Buschinger (1987), together with Peeters and Crozier (1988), have advocated the need to distinguish between morphology and function when describing adult ants. Buschinger and Winter (1976) suggested the terms "gynomorph", "intermorph" and "ergatomorph" to denote "morphological aspect" irrespective of function. Intermorph refers to "all forms between alate females and the ordinary workers", and is used to describe all intercastes, including those capable of reproduction in *Formicoxenus, Leptothorax* sp. A and *Harpagoxenus sublaevis*. It is crucial to realize however that "intermorph" only refers to external appearance, but not internal morphology, e.g. presence of a spermatheca (A. Buschinger, pers. comm.; Peeters and Crozier, 1988). Therefore "intermorph" fails to recognize the difference between ergatoid queens and intercastes, since they are both more or less workerlike in visual appearance. Indeed, the intercastes of *H. sublaevis* or *L. nylanderi,* and the ergatoid queens of *Leptogenys,* have all been termed intermorphs (Heinze and Buschinger, 1987), which obscures their profound biological differences.

A review of the ant literature describing atypical morphological forms in ants reveals a wide variety of terms and usages. Sometimes the same term is used to refer to different phenomena, while one phenomenon is described by different terms depending on the authors. For example, Brian (1979) describes intermediate forms as "intercastes" when they cannot reproduce, and "ergatogynes" when they can; he also uses the latter term to refer to the queens of army ants. "Ergatogyne" has often been used indiscriminately to refer to any adult forms which reproduce and cannot be classified as either workers or winged/dealate queens. It has also been used to describe the mated egg-laying workers (= gamergates) found in various ponerine ants. Thus it is necessary for some existing terms to be discarded, and for the others to be used consistently in all species.

I suggest that the terms "ergatoid queens" and "intercastes" are adequate to describe morphological forms which are neither winged queens nor workers, and "ergatogyne" should be discarded. "Ergatoid" should be used as an adjective describing queens which are permanently wingless. Although Bolton (1986) used "apterous queens" to describe wingless queens exhibiting little or no reduction in the alitrunk sclerites (e.g. in the *Monomorium salomonis*-group), he now believes (pers. comm.) they should also be described as ergatoid. The queens of army ants also belong to the category of ergatoid queens, although "dichthadiiform" describes their extreme morphology. The term "intercaste", which is already widely used in the literature (e.g. Brian, 1955; Plateaux, 1970; Passera, 1984), must be understood to make no reference to function – when intercastes mate and reproduce, this must be specified.

Peeters and Crozier (1988) discussed how current ambiguities in the literature of eusocial insects are an obstacle to the study of patterns and processes of evolutionary change. A wide range of evolutionary modifications in reproductive structure are exhibited in ants, and their correct morphological basis must be recognized. This often requires that more attention be given to the developmental events during larval growth. The distinction between intercastes and ergatoid queens needs to be appreciated in order to study the selective pressures leading to the loss of winged queens in various species.

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