

The Evolution of

Social Behavior in Insects and Arachnids

Edited by

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18 • Morphologically 'primitive' ants: comparative review of social characters, and the importance of queen–worker dimorphism

CHRISTIAN PEETERS

ABSTRACT

Ants that exhibit a relatively large proportion of ancestral morphological traits are commonly believed to exhibit less social complexity. This was examined through a comparative review of *Nothomyrmecia*, *Myrmecia*, and the heterogeneous subfamily Ponerinae. A limited dimorphism between winged queens and workers is a common characteristic of morphologically 'primitive' ants. This has two important consequences: (1) queens are not very fecund, and this is reflected in the small size of colonies (a few dozens to several hundreds of workers); (2) solitary foundresses are unable to rear their first generation of workers without hunting outside their nests. In contrast, some of the 'primitive' species having permanently wingless (= ergatoid) queens exhibit considerably greater fecundity, and colonies reach a few thousands. There is also a small number of permanently queenless ponerine ants, in which one or more mated workers reproduce (several dozens to a few hundreds of workers per colony).

Ecological characteristics of 'primitive' ants include their predatory habits (in addition, sweet secretions are collected in various genera), various degrees of diet specialization, and a widespread lack of cooperation among foragers (although several species with ergatoid queens, and larger colonies, exhibit sophisticated recruitment and even group predation). Role specialization among sterile workers (including the influence of age) follows the typical formicid pattern; polymorphic workers occur in only one species. True trophallaxis among nestmates does not exist (two exceptions only); eggs (either reproductive or trophic) are eaten in several species.

Small colony size influences many ecological characteristics, as well as the ability to produce an appropriate number of sexual individuals annually. Independent foundation in 'primitive' taxa may not always be adaptive, because the dealate queens have to take risks while hunting above ground. The widespread occurrence of colony fission

may be an evolutionary response to this shortcoming. Once there is no longer independent foundation, natural selection can lead either to the production of ergatoid queens, or to the replacement of the queen caste by gamergates.

INTRODUCTION

All ants live in societies in which the majority of female adults are sterile, with only one or a few mated egg-layers. In ants as well as various other social insects (vespine wasps, some bees, and termites), this reproductive division of labor is characteristically based on the production of two distinct female phenotypes: queens and workers. Morphological caste specialization is arguably a key to the ecological success of the Formicidae. An ever-increasing dimorphism between queens and workers has made possible the elaboration of their social organization (Wheeler 1986).

'Primitive' ants is a colloquial expression used here for a number of unrelated taxa that have retained a relatively large proportion of ancestral (plesiomorphic) morphological characters, e.g. *Nothomyrmecia*, *Myrmecia*, *Apomyrma*, and several amblyoponine genera. The tribe Amblyoponini includes the most generalized species in the large subfamily Ponerinae. This review investigates whether morphologically 'primitive' ants also exhibit primitive social characteristics, as is widely believed. All the Ponerinae are included, for comparative purposes. Special emphasis is placed on the extensive secondary modifications in their reproductive biology. Relevant comparisons with 'higher' ants (detailed in Fig. 18-1) are made. I argue that the degree of queen–worker dimorphism provides a useful comparative framework to investigate the various grades of social complexity.

Colonies of the hypothetical ancestral ants presumably consisted of monomorphic females, and reproductive differentiation occurred among these (this is analogous to what occurs in extant polistine wasps, polybiine wasps, and halictine bees). In ants, such ancestral species are extinct, because

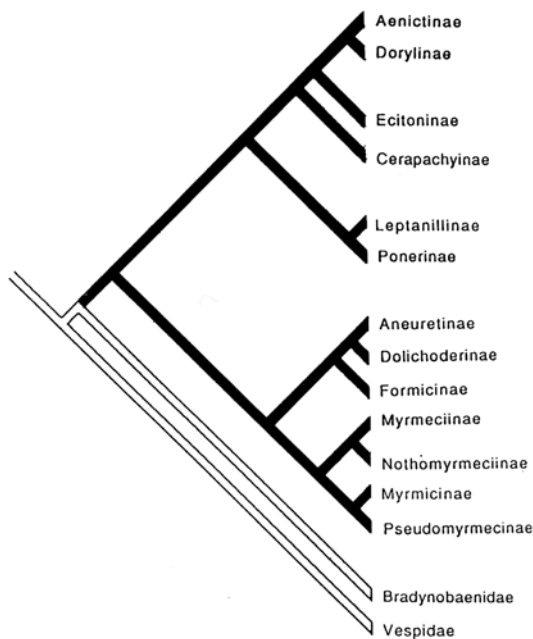


Fig. 18-1. Tentative phylogeny of the Formicidae resulting from a cladistic analysis of the presently recognized ant subfamilies (adapted from Baroni Urbani *et al.* 1992). Two vespid families were included as outgroups. The four uppermost subfamilies constitute the doryline section. Two minor extant subfamilies have been omitted for clarity.

'primitive' species exhibit morphologically distinct queens and workers. Haskins and Haskins (1950a) and Haskins (1970) previously discussed the archaic social structure of *Myrmecia* and various ponerines, including *Amblyopone*. Caryl Haskins was first to recognize that the study of their social profile might give a picture, however imperfect, of the simple stages through which the 'higher' ants have passed in attaining their present remarkably differentiated social organization. Although *Myrmecia* remains poorly studied, the Ponerinae have in recent years become the focus of many investigations (see review of reproductive biology in Peeters 1993). Almost nothing is known about *Apomyrma* (Brown *et al.* 1970). Following Peeters and Crozier (1988), I use the terms 'queen', 'worker' and 'caste' in a strict morphological sense.

INTERNAL PHYLOGENY OF THE ANTS

Brown (1954) divided the Formicidae into two groups of subfamilies, and this basal dichotomy was recently upheld

by a cladistic analysis based on 68 characters (Baroni Urbani *et al.* 1992) (Fig. 18-1). Subfamilies Apomyrminae and Ponerinae belong to one clade, while Myrmeciinae and Nothomyrmecinae belong to the other. These four subfamilies exhibit generalized morphological traits within their respective clades (although they probably no longer resemble the ancestors of the other subfamilies). The findings of Baroni Urbani *et al.* (1992) challenge the idea that *Nothomyrmecia* is the least-specialized living ant, but it remains unambiguous that the poneroid complex diverged from the myrmecoid complex early on. Thus two independently derived 'lower' groups are available to compare and illustrate the progressive elaboration of social structure.

The genus *Myrmecia* is the only extant representative of the subfamily Myrmeciinae. It is endemic to the Australian region, with 90 species currently recognized (Ogata 1991). The monospecific *Nothomyrmecia* has been found only in southern Australia, and is currently placed in a subfamily of its own (Taylor 1978). Myrmeciinae and Nothomyrmecinae appear to be sister groups (Baroni Urbani *et al.* 1992).

The subfamily Ponerinae (1300 species, Bolton 1995) is morphologically very heterogeneous; Bolton (1990b) and Baroni Urbani *et al.* (1992) consider it to be monophyletic, but Hashimoto (1991) and Ward (1994) disagree. Six tribes are currently recognized: Amblyoponini (6 extant genera), Ectatommini (9 genera), Platythyreini (2 genera), Ponerini (23 genera), Thaumatomyrmecini (1 genus) and Typhlomyrmecini (1 genus) (Bolton 1994). The tribe Cerapachyini (e.g. *Cerapachys* and *Sphinctomyrmex*) is no longer included in Ponerinae (Bolton 1990a). A nearly completed revision of tribe Ponerini by William Brown, Jr., will result in the synonymy of several genera under *Pachycondyla* (see Bolton 1994); here, I have used the current traditional names. Ponerine ants flourish world-wide in tropical and subtropical regions, but are poorly represented in the temperate zones. The taxonomic diversity of the Ponerinae is paralleled by very heterogeneous patterns of colony organization, which makes it difficult to distill their essential attributes.

REPRODUCTIVE CHARACTERISTICS OF PONERINAE, MYRMECIA AND NOTHOMYRMECIA

The existence of phenotypically distinct female castes is a hallmark of ant eusociality. Queen-worker dimorphism can be highly pronounced in the advanced subfamilies, but it is

generally small in 'primitive' ants (notwithstanding the absence of wings in workers) (Ponerinae, Brown 1958, 1960, 1976; *Myrmecia*, Haskins and Haskins 1950a; Freeland 1958; Gray 1971c; *Nothomyrmecia*, Taylor 1978). Within the Ponerinae, size dimorphism varies considerably, and reaches a maximum in *Brachyponera lutea* where queens are twice as large as the workers (Haskins and Haskins 1950b). In comparison, myrmecine queens can be up to ten times larger than conspecific workers.

Ovarian specialization

Peeters (1987a) provided the first comparative data on ovarian dimorphism and colony size in Ponerinae, illustrating the importance of specialized queen morphology with respect to egg production. This approach has become common (Villet 1990a; Villet *et al.* 1991; Peeters 1991b; Ito and Ohkawara 1994) and has helped to document considerable interspecific diversity in this subfamily. Many species exhibit little or no difference in the number of ovarioles between the two castes, whereas ovaries are markedly dimorphic in other species (Ponerinae, Peeters 1993; *Nothomyrmecia*, Hölldobler and Taylor 1983; *Myrmecia froggatti*, Ito *et al.* 1994; *M. gulosa*, C. Peeters, unpublished). Caste divergence is even more marked in a few species in which workers lack ovaries (Peeters 1991a; Villet *et al.* 1991; Ito and Okhawara 1994).

A reflection of this limited queen-worker differentiation is the generally low fecundity of ponerine and myrmeciine queens (seldom in excess of 5 eggs per day). In contrast, a monogyne queen of the myrmecine ant *Solenopsis invicta* can lay 150 eggs per hour (Tschinkel 1988).

Associated with limited ovarian dimorphism is the retention of a spermatheca by workers in most ponerine species (Peeters 1991a), as well as in *Nothomyrmecia* (Hölldobler and Taylor 1983) and in at least two species of *Myrmecia* (Crosland *et al.* 1988; Ito *et al.* 1994). Given that ant workers are evolutionarily derived from wasp-like monomorphic females, the presence of a spermatheca in workers can be assumed to be the ancestral condition. The evolution of increasing specialization in the queen caste has often been accompanied by the progressive loss of reproductive attributes in the workers, and thus in 'higher' subfamilies the spermatheca is non-functional or absent in workers. Consequently, they are unable to mate and produce diploid progeny (reviewed in Bourke 1988; Choe 1988). The retention of a spermatheca by workers in many Ponerinae has been highlighted by the occurrence of

worker mating in some species (Table 18-1). Nonetheless, workers lack a spermatheca in other species (Peeters 1991a; Villet *et al.* 1991; Ito and Okhawara 1994). I suggest that the progressive increase in the reproductive specialization of the queen caste eventually eliminated the option of mating by workers, and thus retention of a functional spermatheca was no longer selected for. Ito and Okhawara (1994) offer an alternative interpretation: reduction or loss of worker spermathecae may be a mechanism of 'queen control', but it is not clear how they envisage this.

In 'primitive' taxa, the absence of marked morphological specialization of queens represents the ancestral condition. It also occurs as a secondary modification in representatives of the 'higher' subfamilies (e.g. Formicinae, Formicoxenini (formerly Leptothoracini; Bolton 1994) and *Myrmecina*). In both cases, a limited caste dimorphism imposes constraints on queen behavior during independent colony foundation.

Establishment of new colonies

Colony initiation is a crucial stage in the life history of ants. Independently of workers, a newly mated foundress must find a suitable shelter, lay eggs and rear the first generation of larvae to maturity. In 'higher' taxa, the highly dimorphic queens have large thoraces, and are able to raise their first brood on the metabolic products of wing muscles and fat reserves, as well as storage proteins (Wheeler and Buck 1995). In 'primitive' species, however, the queens' thoraces are not much larger than those of workers, and food must be obtained outside the nest. Thus ponerine and myrmeciine queens establish new colonies in the 'semi-claustral' pattern (Haskins 1970), i.e. they forage above ground at frequent intervals. This exposes them and their brood to predation and accidents. This ancestral condition was first documented in *Myrmecia* and *Amblyopone* in Australia (Wheeler 1933; Haskins and Haskins 1951, 1955). In *Nothomyrmecia*, dealate and inseminated queens have been observed foraging on trees (Hölldobler and Taylor 1983). A similar pattern of colony foundation is exhibited by all the ponerines studied (Kôriba 1963; Colombel 1971; Ward 1981b; Villet 1990d; Villet *et al.* 1989; Dejean and Lachaud 1994). Haskins (1970) reviewed how the 'fully claustral' pattern of colony foundation characteristic of higher ants has been derived through a series of adaptive steps that can still be seen in living ponerine species. In some of these, it appears that the small wing muscles become completely resorbed, and this may partly sustain the founding queen's egg

production. A proportion of these eggs can be fed to the first generation of larvae. In *Pachycondyla apicalis*, 95% of eggs laid during colony foundation are eaten, and furthermore young larvae are cannibalized by older ones (Fresneau 1994). Oophagy seems an essential behavior during colony foundation in 'primitive' ants, and is probably associated with the inability to feed larvae by regurgitation (see below), e.g. *Amblyopone australis* (Haskins and Haskins 1951), *Brachyponera senaarensis* (Dejean and Lachaud 1994), *Ectatomma ruidum* (Corbara 1991), *Plectroctena mandibularis* (Villet 1991a) and *Rhytidoponera confusa* (C. Peeters, unpublished). In the laboratory, an *Odontomachus* foundress was prevented from obtaining outside food, but her larvae continued to develop (Haskins and Haskins 1950a), which also suggests the occurrence of egg cannibalism. Fresneau (1994) suggests that the recycling of the founding queen's eggs reduces her need to forage above ground frequently. The only report of a ponerine queen able to start colonies without periodic provisioning of the larvae from outside sources is *Brachyponera lutea* (Haskins and Haskins 1950b), although the manner of larval feeding (oophagy or regurgitation) remains unclear. Not surprisingly, the large difference between queen and worker statures in *B. lutea* is exceptional in the Ponerinae. Caste differentiation is also pronounced in *Paltothyreus tarsatus*, where new queens have large fat reserves when they disperse (Braun *et al.* 1994b).

Fully claustral foundation is impossible in 'primitive' ants owing to the morphological limitations of queens. The conversion of body tissues into food for the first larvae was a vital evolutionary advance in the Formicidae (Hölldobler and Wilson 1990). However, founding queens also forage in various species belonging to two advanced subfamilies (Formicinae: *Cataglyphis bicolor* (Fridman and Avital 1983), *Polyrhachis laboriosa* and *P. militaris* (Lenoir and Dejean 1994); Myrmicinae: *Acromyrmex versicolor* (Rising *et al.* 1989), *Manica rubida* (Le Masne and Bonavita 1969), tribe Dacetini (Dejean 1987)). Because related species exhibit the fully claustral pattern, it seems clear that this is a secondary modification, presumably as an adaptation to local ecological conditions.

Evolution of flightless queens

Although ant workers are always characteristically wingless, ant queens usually have wings. These enable aerial dispersal and colonization of new habitats, and furthermore the wing muscles constitute a metabolic reserve during colony foundation. Despite these obvious adaptive

benefits, a permanently wingless queen caste has evolved in a significant number of ants. Such 'ergatoid' queens (Bolton 1986; Peeters 1991b; Villet 1989) exhibit substantial modifications in their external appearance, because the loss of flight muscles causes their thorax to resemble that of workers (especially in species where queen stature is similar to the workers'). Ergatoid queens exist in all subfamilies, and are the exclusive form in subfamilies belonging to the doryline section (see Fig. 18-1).

Ergatoid queens occur widely in the Ponerinae (12 genera in four tribes; Table 18-1). In *Nothomyrmecia*, queens have very short wings, which appear unsuitable for flying; this brachyptery has not been accompanied by a simplification of the flight sclerites (Taylor 1978). In the genus *Myrmecia*, both brachypterous queens and ergatoid queens occur in addition to normal winged queens (McAreavey 1948; Clark 1951), but their biology and taxonomic occurrence is poorly known. The evolution of ergatoids is often associated with significant modifications in colony organization. Fission occurs instead of independent foundation, i.e. a mother colony becomes divided into two autonomous groups. Ergatoids in various species have much larger ovaries than their workers, despite similar body sizes. Bigger colonies are a consequence of this greater egg-laying specialization (Peeters 1993). The evolution of ergatoids in the Ponerinae has sometimes reached an extreme condition where queens have hypertrophied gasters as an adaptation for the concurrent maturation of large numbers of eggs (for example, in *Simpelta* (Gotwald and Brown 1966)). However, ergatoids retain a relatively low fecundity in other ponerine species (even in some *Leptogenys*), with colonies of fewer than 100 workers (Peeters 1991b).

Comparative data on queen modification in 'primitive' taxa can help understand why wings were lost. *Myrmecia regularis* represents a possible intermediate stage in the evolutionary transition. Queens are winged (although wing development varies between populations), but they dealate *before* dispersal from the parental nest (Haskins and Haskins 1955). Once mated, they found colonies in the partially claustral manner. Wings are thus no longer essential in *M. regularis*, although wing muscles may be. In other species exhibiting a similar behavior, the development of wings may have been selected against. Support for this evolutionary pathway comes from limited laboratory results on the ponerine *Plectroctena mandibularis* (Villet 1991a). An alternative hypothesis (Peeters 1990) is that independent foundation is first replaced by colony fission, and then followed by loss of wings in queens.

Table 18-1. *The occurrence of different morphological types of reproductives in subfamilies Nothomyrmecinae, Myrmecinae and Ponerinae*

Only 18 ponerine genera are included; in another 24 genera, only alate queens have been reported. References on ergatoid queen morphology (either taxonomic or biological studies) are listed in Peeters (1991b, 1993); see also Clark (1951); Ito and Ohkawara (1994). AQ, alate queens; AQ*, brachypterous queens; EQ, ergatoid queens; G, gamergates only; Q+ G, both dealate queens and gamergates reproduce.

Genus	Reproductives	Key references (gamergates only)
<i>Nothomyrmecia</i>	AQ*	—
<i>Myrmecia</i>	AQ, AQ*, EQ	—
Tribe Amblyoponini (6 genera)		
<i>Amblyopone</i>	AQ, G	Ito 1993a
<i>Onychomyrmex</i>	EQ	—
Tribe Ectatommini (9 genera)		
<i>Discothyrea</i>	AQ, EQ	—
<i>Gnamptogenys</i>	AQ, EQ, G	Gobin <i>et al.</i> 1994
<i>Heteroponera</i>	AQ, EQ	—
<i>Proceratium</i>	AQ, EQ	—
<i>Rhytidoponera</i>	AQ, G, Q+G	Haskins & Whelden 1965; Ward 1981b, 1983, 1984; Peeters 1987b
Tribe Platythyreini (2 genera)		
<i>Platythyrea</i>	AQ, EQ, G, Q+G	Villet 1991b,c, 1993; Villet <i>et al.</i> 1990; Itô 1995
Tribe Ponerini (23 genera)		
<i>Diacamma</i>	G	Fukumoto <i>et al.</i> 1989; Peeters & Higashi 1989; Peeters <i>et al.</i> 1992
<i>Dimoponera</i>	G	Haskins & Zahl 1971; Paiva & Brandão 1995; Araujo <i>et al.</i> 1990
<i>Harpegnathos</i>	Q+ G	Peeters & Hölldobler 1995
<i>Hypoponera</i>	AQ, EQ	—
<i>Leptogenys</i>	AQ, EQ, G	Ito & Ohkawara 1994; Davies <i>et al.</i> 1994
<i>Pachycondyla</i>	AQ, G, Q+ G	Peeters & Crewe 1986; Peeters <i>et al.</i> 1991; Sommer & Hölldobler 1992; Ito 1993c
<i>Hagensia</i> ^a	G	Villet 1992
<i>Megaponera</i> ^a	EQ	—
<i>Ophthalmopone</i> ^a	G	Peeters & Crewe 1985a, 1985b
<i>Plectroctena</i>	AQ, EQ	—
<i>Ponera</i>	AQ, EQ	—
<i>Simopelta</i>	EQ	—
<i>Streblognathus</i>	G	Ware <i>et al.</i> 1990

^a Synonymized under *Pachycondyla* (see Bolton 1994).

Evolutionary loss of the queen caste

In various ponerine tribes and genera, workers reproduce instead of the queens, which are no longer produced (Table 18-1). Several aspects of the biology of queenless ants have been reviewed (Peeters 1991a, 1993). Colonies typically consist of a few dozen workers. 'Gamergates' (mated reproductive workers) are less fecund than queens

of related species, and they have shorter lifespans. Fission is the obligatory mode of colony reproduction, because gamergates lack the necessary opportunities for independent foundation. In a few ponerine ants both queens and gamergates reproduce (Table 18-1).

Queenless ponerine species are unique among the ants, because all female inhabitants of a colony are able to mate and produce eggs. Nevertheless, only one or a

few workers reproduce. Such absence of specialized reproductive traits is analogous to the situation in various polistine wasps and halictine bees, although in Ponerinae it is a secondary modification (Peeters and Crozier 1988). This reproductive organization is akin to the cooperative breeding documented in various vertebrates, such as naked mole rats, wild dogs and dwarf mongooses (Sherman *et al.* 1991; Jennions and Macdonald 1994). Crespi and Yanega (1995) have advocated that the term 'eusociality' be restricted to societies in which reproductive individuals are 'irreversibly behaviorally distinct prior to reproductive maturity'; I understand this differentiation to be the consequence of morphological specialization, otherwise it cannot be irreversible. This new definition changes the traditional scope of eusociality, and accordingly queenless ponerine ants, together with various social wasps and bees, are excluded. Their societies, entirely made up of *totipotent* individuals (i.e. having the potential to express the full behavioral repertoire of the population, and the ability to produce offspring like oneself (Crespi and Yanega 1995)), are better described as 'cooperative breeders'. This contrasts with eusocial ants, which have mutually dependent queens and workers (the latter are not totipotent).

As in cooperatively breeding mammals, dominance hierarchies in queenless ants function to regulate sterility of group members. Physical confrontation among the workers leads to the inhibition of ovarian activity in subordinates, and sometimes it regulates mating as well (Heinze *et al.* 1994). In some species there is always only one gamergate per colony; other queenless species are polygynous (Peeters 1993).

Gamergates have never been reported outside the Ponerinae. They may be expected to occur in *Myrmecia*, since workers seem morphologically competent to replace queens. Indirect evidence suggests that gamergates should be looked for in *Nothomyrmecia* as well; an electrophoretic analysis of gene-enzyme variation revealed that intracolony relatedness was lower than that predicted with a single, once-mated queen (Ward and Taylor 1981).

Another two novel reproductive modifications have recently been reported in the Ponerinae. In *Pachycondyla obscuricornis*, reproductive 'intercastes' (*sensu* Peeters 1991b, i.e. phenotypic intermediates between queens and workers) were found in a queenless colony (Düßmann *et al.* 1996). In *Platythyrea punctata*, virgin workers are able to produce diploid offspring from unfertilized eggs (Heinze and Hölldobler 1995).

ECOLOGICAL CHARACTERISTICS OF PONERINAE, MYRMECIA AND NOTHOMYRMECIA

Colony size

In contrast to the huge colonies often encountered in the advanced subfamilies (see, for example, Hölldobler and Wilson 1990, Table 3-2), small colonies prevail in 'primitive' taxa. In *Nothomyrmecia*, mature nests contain 50-70 workers (Taylor 1978). In *Myrmecia*, colonies often consist of a few hundred workers, but in some species mature colonies are much smaller (Haskins and Haskins 1950a; Gray 1974; Itô *et al.* 1994). Colonies of 1000-3000 workers have been found in the larger species of *Myrmecia* (Gray 1974; Higashi and Peeters 1990). In the Ponerinae, colonies have several dozens to hundreds of workers (reviewed in Peeters 1993), with the smallest societies known in ants (9 ± 3 workers) occurring in *Pachycondyla sublaevis* (Peeters *et al.* 1991). Nevertheless, the colonies of a minority of ponerines can contain a few thousand individuals. *Leptogenys distinguenda* is exceptional, with colonies of up to 50 000 workers (and one ergatoid queen) (Maschwitz *et al.* 1989). This may even be exceeded by *Pachycondyla luteola*, where single colonies can be the exclusive inhabitants of individual *Cecropia* trees 30-35 m high (Davidson and McKey 1993; Verhaagh 1994).

Colony size is a reflection of both queen fecundity and average worker longevity. The egg-laying rate of queens determines the upper limit on colony growth, but a further consideration is that enough food must be available for the larvae. Workers in 'primitive' taxa are generally large (length reaches 30 mm in some genera, although in others it is as small as 1.7 mm), and this larger body size may be correlated with greater longevity.

Diet specialization

All 'primitive' ants are armed with a sting and hunt arthropods. Although many ponerines are opportunistic in their choice of prey, others are very prey-specific, e.g., *Amblyopone pluto* on geophilomorph centipedes (Gotwald and Léveux 1972), neotropical *Gnamptogenys* spp. on millipedes (Brown 1992), *Proceratium* on spider eggs (Brown 1979), *Leptogenys* sp. 13 (near *kraepelini*) on earwigs (Steghaus-Kovac and Maschwitz 1993) (see also Hölldobler and Wilson 1990, Table 15-1). The genus *Leptogenys* displays several degrees of prey specialization: some species are generalists preying on a wide taxonomic and size range of

arthropods, whereas others are narrowly specialized isopod or termite hunters (Steghaus-Kovac and Maschwitz 1993). Scavenging on dead arthropods can be important in a few genera. In *Pachycondyla apicalis*, 45% of items retrieved to the nests were freshly killed prey (with lepidopteran larvae predominating), and as many items were dead insects (Fresneau 1994).

Despite this carnivorous propensity, a few ponerines (belonging mostly to tribe Ectatommini) depend partly on other sources of food. *Paraponera clavata* forage on the foliage of the rainforest understory, in search of arthropod prey as well as sugary secretions from extrafloral nectaries (Young 1977). In *Ectatomma ruidum*, some foragers in a colony are specialized on the nectaries of an orchid, while others hunt (Passera *et al.* 1994). A few generalized ground predators also utilize honeydew from homopterans, and receive secretions from butterfly larvae. *E. ruidum* tend membracids (Weber 1946), as well as myrmecophilous lycaenid and riodinid caterpillars (Robbins 1991; DeVries 1988). *Odontomachus troglodytes* can climb cocoa trees for a short distance to find aphids and coccids, and often construct crude shelters of soil particles over them (Evans and Leston 1971). *O. troglodytes* also attend lycaenid caterpillars (Lamborn 1915). Species in the *Rhytidoponera impressa* group tend homopterans (Ward 1981a); *R. 'metallica'* attend lycaenid larvae (Common and Waterhouse 1981).

In Mexican rainforests, some species of both *Odontomachus* and *Pachycondyla* are highly attracted to the seeds of various herbs; these are retrieved to the nest where the elaiosomes (fleshy appendages containing lipids) are eaten, after which the seeds are discarded (Horvitz and Beattie 1980). *Rhytidoponera* sp. 12 (near *mayri*) has a similarly important role as seed dispersers in the dry sclerophyllous scrub of Australia (Davidson and Morton 1981). In contrast, various other species of *Rhytidoponera* and *Heteroponera* opportunistically consume seeds (Andersen 1991). *Brachyponera senaarensis* is also able to eat seeds. Its diet varies seasonally and geographically: in humid tropical regions of Africa, both seeds and insect prey are collected during the rainy season, whereas the diet consists exclusively of seeds during the dry season, which lasts three months (Dejean and Lachaud 1994). In dry tropical regions, however, foragers react to the absence of seeds in the rainy season by adopting a 100% animal diet (Lévieux 1979). The neotropical *Pachycondyla luteola* feeds mostly on glycogen-rich Müllerian bodies at the base of petioles of young leaves (Davidson and Fisher 1991; Verhaagh 1994).

Myrmecia ants also hunt a variety of insects (including flies and honey bees), but only when larvae are present in the nests. When these are absent, workers forage for nectar almost exclusively (Haskins and Haskins 1950a; Gray 1971b, 1974). *M. desertorum* attend homopterans (Gray 1971b). *Nothomyrmecia* workers forage exclusively at night, climbing low *Eucalyptus* trees where they search for various small insects as well as sweet substances (Taylor 1978).

The predatory habits of 'primitive' ants are shared with their wasp ancestors (e.g. Scoliidae, Tiphiidae). Many Ponerinae hunt a wide range of invertebrates opportunistically, and the extreme prey specialization of some species appears to have evolved secondarily. Indeed it is also exhibited in some myrmecine ants (Hölldobler and Wilson 1990, Table 15-1).

Foraging habits

Many species of ponerine hunt alone (reviewed in Peeters and Crewe 1987). There is no cooperation among foragers, either through the transfer of information about the location of new sources of prey, or through direct assistance during the killing and retrieving of prey. Solitary foraging and the absence of recruitment trails have also been documented in *N. macrops* (Hölldobler and Taylor 1983), as well as in all the species of *Myrmecia* investigated by Haskins and Haskins (1950a) and Gray (1971b). Solitary predation contrasts with the elaborate systems of recruitment and cooperative hunting displayed by other ponerine ants. These include army ant-like swarm raiding in *Onychomyrmex* and some species of *Leptogenys* (Hölldobler *et al.* 1982; Maschwitz *et al.* 1989; Duncan and Crewe 1994), or the invasion of a termite nest by a column of hundreds of workers in *Megaponera foetens*, following its location by a single scout ant who lays a trail back to her nest (Longhurst and Howse 1979).

Peeters and Crewe's (1987) comparative overview of foraging in the Ponerinae emphasized that the occurrence of simple and complex hunting strategies does not reflect phylogenetic relationships. Trail communication has evolved many times independently; and four different trail-pheromone glands have been identified in the Ponerinae (Hölldobler and Wilson 1990). Foraging characteristics seem to result from the unique selective pressures facing each species; for example, in the tribe Ponerini, all species examined have the exocrine glands necessary for recruitment, but only some of them hunt in groups. Together with ecological considerations and the extent of prey specificity, colony size seems an important factor (Beckers *et al.*

1989), i.e. ponerine species with small colonies are not likely to raid in groups. In *Amblyopone*, species that do not recruit have colonies with only one or two dozen workers, but one species from the *reclinata* group, which is able to retrieve centipedes cooperatively, has 100 workers per colony (see Ito 1993b). Similarly, the entire spectrum of foraging strategies is exhibited in *Leptogenys*. In a guild of 12 species studied by Maschwitz *et al.* (1989), five have large colonies and are group- or swarm-raiders, whereas the other species search for prey solitarily (after encountering prey, they either recruit a group of nestmates, or attack and retrieve the prey alone). A cladistic analysis of 22 ant species (Baroni Urbani 1993) also showed that differences in recruitment behavior do not reflect phylogeny, but rather represent species-level adaptations to environmental conditions.

Nesting requirements

All *Myrmecia* spp. nest in the ground except *M. mjobergi*, which constructs its nest in trees (Clark 1951). Founding queens of various species all construct similar simple nests, but as the colonies grow larger, each species exhibit a typical design (Gray 1971a, 1974). Several larger-sized *Myrmecia* have big conspicuous soil mounds, which reach 0.7 m in height in *M. brevinoda* (Higashi and Peeters 1990). Short-lived nests have not been reported in this genus.

The nests of many Ponerinae also occur in the ground; large or small chambers, connected together by galleries, are superficial or extend to considerable depths. Various species invest much labor in building permanent nests; for example, finely shaped chambers in *Centromyrmex sellaris* (Lévieux 1976a), flood-resistant earthen spheres in *Harpegnathos saltator* (Peeters *et al.* 1994), extensive networks of shallow foraging galleries in *Paltothyreus tarsatus* (Braun *et al.* 1994a). In contrast, other species cannot dig their own nests, and are only able to make limited modifications to pre-existing structures; for example, *Amblyopone mutica* reutilizes underground networks of empty cavities (e.g. roots, termite galleries) (Lévieux 1976a). Similarly, *Pachycondyla apicalis* occupies the abandoned galleries made by passalid beetles in rotting wood (Fresneau 1994). Many ponerines inhabit mesic to humid forests, and have ephemeral nests in the leaf-litter stratum, for example, inside or under decaying plant material, under stones, in crevices or in fallen cocoa pods (see Wilson 1959). The dichotomy between permanent and short-lived nests is not related to colony size. *Dinoponera australis* has very

small colonies (13 ± 6 workers), yet its nests often reach one meter in depth (Paiva and Brandão 1995). In contrast, *Leptogenys chinensis* (200–300 workers per colony) nests in any available cavities near the ground (Maschwitz and Schönegege 1983).

Very few ponerine ants make arboreal nests; examples are *Gnamptogenys menadensis* in Indonesia (Gobin *et al.* 1994), *Platythyrea conradti* in Cameroun (Lévieux 1976b), and *Pachycondyla goeldii* in French Guyana (Corbara and Dejean 1996). *Pachycondyla luteola* colonizes exclusively the hollow stems of *Cecropia* trees (Davidson and Fisher 1991; Verhaagh 1994).

A polydomous organization (i.e. a single colony distributed into several distinct nests) has only been reported in *Platythyrea conradti* (Lévieux 1976b) and *Ophthalmopone berthoudi* (Peeters and Crewe 1987).

Frequent nest emigration

Most ants are able to shift their nest site if it becomes unsuitable. Although this behavior has only been reported in one species of *Myrmecia* (Gray 1971b), it is especially ubiquitous in ponerine genera. When nests are ephemeral, or become too small, the ants emigrate elsewhere, e.g. *Rhytidoponera* species in the *impressa* group (Ward 1981a), *Diacamma* sp. from Japan (Fukumoto and Abe 1983). Emigration is efficiently organized in *Megaponera foetens*, where ants and brood move in a distinct column to new sites up to 50 m away (Longhurst and Howse 1979). In *Leptogenys chinensis*, nests are abandoned after about two weeks, and relocation can occur to a new site just a few meters away (Maschwitz and Schönegege 1983). Frequent nest emigrations are often characteristic of species exhibiting colony fission and ergatoid queens. *Pachycondyla marginata* is thus exceptional for a migratory species, because it has winged queens (colonies consist of 500–1500 workers) (Leal and Oliveira 1995).

Army ant (legionary) behavior

Legionary behavior consists of two fundamental features: migration and group predation (Wilson 1958). This characteristic of the doryline and ecitonine ants occurs to a limited extent in a few ponerine genera, i.e. *Onychomyrmex* (Wilson 1958; Hölldobler and Wilson 1990), *Simopelta* (Gotwald and Brown 1966), and some species of *Leptogenys*. Nests are very temporary in aspect, consisting of nothing more than preformed cavities in rotting logs or simple bivouacs in open leaf litter. Legionary behavior is

best documented in *L. distinguenda*, where groups of more than 20 000 workers conduct nocturnal raids (Maschwitz *et al.* 1989). Raids are not directed to specific food sources by scouts; nestmates move around in a group and, upon finding prey, immediate cooperation ensures efficient attack. Migrations occur every 1–3 days, usually to an area (5–59 m away) that has just been raided.

Group-raiding ants can feed on large arthropods or the brood of other social insects, which are not normally accessible to solitary foragers. Legionary behavior thus enables great ecological diversification. Indeed, *L. distinguenda* has filled the ecological niche of doryline ants in southeast Asia (Maschwitz *et al.* 1989). All legionary ponerine species have ergatoid queens and large colonies. Unlike many true army ants, the development of brood is not synchronized with the migration events.

INTRACOLONIAL ORGANIZATION

Patterns of food exchange

Trophallaxis

The sharing of food among colony members is an integral part of the specialization of roles associated with sociality (reviewed in Wheeler 1994). After food is brought into the nest by the foragers, it is consumed by those colony members who are not active outside. The most sophisticated form of food sharing is trophallaxis, which is widespread in some groups of advanced ants (Formicinae, Dolichoderinae and Myrmicinae). Following appropriate tactile signals with the antennae and forelegs, a solicited worker regurgitates a drop of liquid from her crop (anterior to the midgut), and this is imbibed by the begging ant. In these advanced groups, larvae are fed exclusively with regurgitated liquid food. In the 'primitive' ants, however, trophallaxis is known in only two species. All colony members, larvae included, feed directly on the arthropod prey retrieved to the nest (larvae have a flexible thorax which allows much movement, and sometimes they are able to crawl within the nest, e.g. *Amblyopone pluto* (Gotwald and Lévieux 1972)). A possible evolutionary precursor of true trophallaxis has been observed in several ponerines, which transport liquids between their mandibles (Fresneau *et al.* 1982; Hölldobler 1985). Foragers exploiting extrafloral nectaries, or aphids and coccids, return to their nest with a droplet of sugary liquid held *outside* their mouths, and this is then shared with nestmates. There is thus no regurgitation from the crop in this 'pseudotrophallaxis',

but the accompanying tactile signals are similar to those observed during regurgitation in 'higher' ants (Hölldobler 1985). Earlier accounts of trophallaxis in *Myrmecia regularis* (Haskins and Whelden 1954) and in various ponerines (Le Masne 1952; Haskins 1970) may have overlooked this distinction. Nevertheless, the regular occurrence of true trophallaxis has recently been documented in *Ponera coarctata* (Liebig *et al.* 1994) and *Hypoponera* sp. (Hashimoto *et al.* 1995).

Egg cannibalism

A different form of intracolony food exchange is oophagy, which occurs in a wide diversity of ants (reviewed in Crespi 1992; Wheeler 1994). Whether this involves normal reproductive eggs, or special immature oocytes instead, is an important distinction. Typically, the latter ('trophic eggs') lack a chorion and are flaccid, and they differ in shape and histology from reproductive eggs (Passera *et al.* 1968; but see Voss *et al.* 1988). Irrespective of this distinction, oophagy frequently involves worker-laid eggs, which emphasizes that the functional ovaries of workers can play an important social role. This may be especially important in 'primitive' taxa: because the workers do not regurgitate to the larvae or the queen, they can store reserves and utilize them to produce immature oocytes.

Consumption of eggs has been observed in *Nothomyrmecia* (Hölldobler and Taylor 1983) and several *Myrmecia* species (Haskins and Haskins 1950a; Crosland *et al.* 1988). In *M. forceps* and *M. gulosa*, workers lay trophic eggs which are fed to the larvae or the queen (Freeland 1958). However, oophagy seems restricted to a proportion of ponerine genera (albeit distributed in three tribes). In *Amblyopone silvestrii*, reproductive eggs laid by queens are consumed by first and second instar larvae (Masuko 1990). In *Prionopelta amabilis*, the queen is reported to feed almost exclusively on worker-laid eggs (Hölldobler and Wilson 1986). In *Ectatomma*, trophic eggs are laid by workers and differ in color from reproductive ones (Weber 1946; C. Peeters, unpublished data). In *Gnamptogenys menadensis* (with gamergates), virgin workers produce trophic eggs; these are shorter than reproductive eggs and are fed to the larvae (Gobin *et al.* 1994). In various species of the permanently queenless genus *Diacamma*, cannibalism of reproductive eggs laid by virgin workers is part of the behavioral mechanism of hierarchy formation (Peeters *et al.* 1992; Peeters and Tsuji 1993). In *Pachycondyla obscuricornis*, young virgin workers lay eggs in queenright colonies, and these are eaten

by the queen and larvae (Fresneau 1984). In orphaned colonies of both *P. obscuricornis* and *P. apicalis*, eggs produced by workers (and dealate virgin queens in *P. obscuricornis*) are destroyed during dominance interactions (Oliveira and Hölldobler 1990, 1991). In the permanently queenless *P. krugeri*, virgin workers lay trophic eggs, which are often fed to the larvae (Villet and Wildman 1991). In *Ponera pennsylvanica*, workers occasionally lay small, sticky eggs, which are subsequently eaten or fed to larvae (Pratt *et al.* 1994).

Egg cannibalism thus occurs in two distinct contexts: trophic eggs are consumed as a strategy of nutrient exchange among nestmates, whereas the destruction of reproductive eggs can be a form of dominance interaction, with incidental trophic benefits for the dominant individuals. Data from various 'primitive' ants do not contradict the general formicid rule that the less frequent the exchange of liquid food by regurgitation, the more frequent the exchange of trophic eggs (Hölldobler and Wilson 1990), although several species seem to lack both behaviors. Eggs may also function in food transfer during the initial stage of colony foundation, but in contrast to the above instances of worker-laid reproductive eggs, the queen's fertilized eggs are involved. Egg consumption by colony-founding queens is not unique to the 'primitive' taxa, however (see, for example, *Solenopsis invicta*, Voss *et al.* 1988; *Atta*, Hölldobler and Wilson 1990; see also Wheeler 1994).

The lack of trophallaxis in 'primitive' ants may contribute to the low fecundity of queens, although this awaits empirical documentation. Reproductives in a colony often have to compete with their nestmates while feeding on prey items. One exception is *Amblyopone silvestrii*, where the queen feeds exclusively on hemolymph from last-instar larvae (which is obtained after biting them) (Masuko 1986). A similar behavior may occur in *Mystrium mysticum* (Wheeler and Wheeler 1988).

Division of labor

Division of colony labor contributes to the ecological success of social insects by enhancing the efficiency and reliability of colony responses to important contingencies (Hölldobler and Wilson 1990). Numerous studies have shown that complicated social organization is attained with a relatively simple repertoire of individual behaviors (reviewed in Robinson 1992). Any empirical description of polyethism proceeds by the following steps: (1) establish that there is role specialization among workers, i.e.

individuals perform only one activity for a sustained period of time; (2) establish whether roles are performed in a predictable temporal sequence (i.e. workers pass through distinct behavioral phases during their lives). Ponerine and myrmecine ants are ideal subjects to investigate division of labor because their colonies are small, making it possible to study the behavior of all workers as individuals (the workers (often large) are easily marked with paint or numbers). As a consequence, their activities in the colony can be followed with unequalled detail, and the pattern of polyethism may be better understood in the Ponerinae than in any other subfamilies (in contrast, very little is yet known about *Myrmecia*). Polyethism was first demonstrated in ponerines by Bonavita and Poveda (1970).

Behavioral profile of reproductives

All ponerine foundresses initially exhibit a full complement of behaviors, especially since they need to forage outside. Later in colony ontogeny, their repertoire decreases, and important interspecific differences appear. Foundresses of *Pachycondyla apicalis* continue to forage for a while after emergence of the first workers, and they always remain involved in brood care (Fresneau *et al.* 1982). In contrast, queens of *Ectatomma ruidum* are immobile over eggs and larvae, but do not attend them (Corbara 1991). Similarly, the queens of *Ponera pennsylvanica* do not care for brood at all (Pratt *et al.* 1994). There seems to be a comparative trend that queens are less active (oviposition excepted) with increased caste dimorphism, and thus become more behaviorally distinct from workers. The ergatoid queen of *Megaponera foetens* is highly fecund (33 eggs per day); she does little else in the colony, and is surrounded by a distinct retinue of workers (Hölldobler *et al.* 1994). In contrast, queens attract little attention in *E. ruidum* (Corbara *et al.* 1989), *P. apicalis* (Fresneau 1994) and *Nothomyrmecia macrops* (Jaisson *et al.* 1993).

As in some advanced ants (e.g. *Acromyrmex versicolor*, *Linepithema humile*), winged ponerine queens who cannot mate remain in the colonies and participate in maintenance activities (including foraging), e.g. *Harpegnathos saltator* (C. Peeters, unpublished), *Odontomachus affinis* (Brandão 1983), *Pachycondyla apicalis* (Fresneau 1994), *Rhytidoponera confusa* (Ward 1981b).

Not unlike queens, gamergates usually have a behavioral profile distinct from that of sterile workers, although there is much interspecific variation (Villet 1990c, 1991b,c; Ware *et al.* 1990). In contrast to sterile workers, gamergates do not become active outside the nest as they become older.

Role specialization among infertile workers

The investigation of various species belonging to *Ectatomma* and *Pachycondyla* has shown that there is no rigid pattern of division of labor, and this accounts for the occurrence of variations between conspecific colonies. Corbara (1991) documented in *E. ruidum* how the stability of social organization contrasts sharply with the flexibility of role specialization in individuals. There is a distinct chronology in the appearance of functional specializations, but the actual time spent in each functional group seems variable from one individual to another (Corbara *et al.* 1989). A similar pattern is found in *E. tuberculatum*; older workers can revert to brood care if there is a colony need for it (Fénéron 1993). In *P. apicalis*, most workers can be described by three profiles (brood care; non-social activities inside nest; foraging), with remaining individuals having intermediate status (Fresneau and Dupuy 1988). In *Amblyopone silvestrii*, tasks inside the nest are spatiotemporally connected; for example, the dismembering of prey and placing it near larvae, as well as the cleaning of larvae, are often performed by the same workers (Masuko 1996). Thus task specialization is weakly defined, with the exception of foraging. Similarly, in *Nothomyrmecia*, all colony members participate to some extent in all the activities (Jaisson *et al.* 1993). Ethograms of species with gamergates (Villet 1990c, 1991b,c; Villet and Wildman 1991) indicate that conventional role specialization occurs among the infertile workers, and is not based on size differences. Interspecific comparisons are often hindered by methodological variations between researchers.

In newly established colonies, the first generation of workers are remarkably flexible in the performance of the various essential tasks (Lachaud and Fresneau 1987; Corbara 1992; Fresneau 1994). Owing to a pattern of brood cannibalism, new workers do not emerge continuously, but rather in temporal clusters, and they specialize according to the colony needs at the time. Consequently, workers in the same age cohort can follow several different courses of polyethism (Fresneau 1994).

Influence of age on polyethism. Polyethism associated with age is generally observed throughout the social insects (Hölldobler and Wilson 1990, Table 8-3): workers labor in the nest when they are young, and forage outside when they are older. Investigations of advanced ants have generally relied on the color differences among adults (degree of pigmentation of body parts increases with age), and thus

groups of individuals are observed. However, in many studies of ponerine species, the exact age of various numbers of nestmates has been known, and their lifetime profile documented.

Traniello (1978) claimed that groups of age-related task specialists do not exist in *Amblyopone pallipes*. Although this has been widely cited as new evidence of the simple nature of sociality in 'primitive' ants, Traniello's data should be critically examined. His conclusion that there is little role specialization among nestmates was based on a single colony, in which the age of workers was unknown. Indeed, the lack of age polyethism was inferred from separate observations that '5 days-old callows leave the nest to hunt'. Lachaud *et al.* (1988) also investigated polyethism in *A. pallipes* (one colony studied) and documented limited role specialization. However, such behavioral plasticity is similar to what is observed among the first brood of workers during colony foundation in other ponerines. Furthermore, Masuko (1996) studied two colonies of *A. silvestrii* in which the age of most individuals was known, and convincingly demonstrated that role specialization is based on age.

Traniello (1978) explained his singular results by invoking the small size of colonies in *A. pallipes*, together with the occurrence of a single brood per year (apparently an adaptation to survive the long winter in the cool moist forests of the eastern USA and Canada). However, *Ponera pennsylvanica* is another temperate ponerine where a single cohort of workers ecloses nearly simultaneously, and Pratt *et al.* (1994) documented the existence of functional groups of workers, although highly variable in their composition. Pratt *et al.* (1994) also obtained additional data on age polyethism, as have Hölldobler and Wilson (1986) in *Prionopelta amabilis*, Villet (1991c) in *Platythyrea schultzei*, Dejean and Lachaud (1994) in *Brachyponera senaarensis*, and Pratt (1994) in *Gnamptogenys horni*.

Influence of size polymorphism on polyethism. Only a minority of advanced ants have polymorphic workers (Hölldobler and Wilson 1990, Table 8-2), and this is always associated with role specialization. In almost all ponerine and myrmecine species, discrete morphological subcastes are absent among workers. Size variation has been recorded, but this is not necessarily associated with polymorphism, which occurs when individuals at the extremes of the size range exhibit distinctly different proportions in body shape ('allometry'). Only in *Megaponera foetens* do workers exhibit both size variation and allometry (Crewe *et al.* 1984); there is an interesting difference in their tempo of activity (majors

perform 135 acts per hour, and minors 248 (resting behaviors excluded) (Villet 1990b)), as well as in their energetic cost of retrieving prey (Duncan 1995). In a field study of raiding behavior in *M. foetens*, Longhurst and Howse (1979) showed that minors enter termite galleries and immobilize prey by stinging, and majors carry bundles of termites back to the nest. Furthermore, scout ants are always majors. Workers of *Paraponera clavata* exhibit limited unimodal variation in size, and this is statistically associated with task performance (foraging vs. brood care), although the size distributions of workers performing different tasks overlap almost completely (Breed and Harrison 1988). Claims of weak allometry in *P. clavata* are not supported by the published data (D. Wheeler, personal communication).

Intracolony variation in the size of workers is especially marked in many of the larger species of *Myrmecia*, although they remain monomorphic (Gray 1971c). In *M. brevinoda*, worker lengths range bimodally from 13 to 36 mm, but this variation is not associated with allometric differences in the shape of body parts (Higashi and Peeters 1990). None the less, such size differences are the basis of polyethism among the workers: hunting, defense and extranidal building were done mainly by large workers of *M. brevinoda*, whereas smaller workers performed intranidal building (Higashi and Peeters 1990).

CONCLUSIONS

The pattern of division of labor in 'primitive' ants seems to differ little from that in 'higher' taxa with monomorphic workers. The behavioral characteristics of individuals are similar to that observed in advanced subfamilies. Individual variability is conspicuous in various Ponerinae, but this may be due to the small worker populations. Age polyethism seems to have been a general phenomenon ever since the inception of sociality in the ants.

The evolution of specialized queen morphology

A tremendous diversity of ecological and reproductive strategies are exhibited in myrmeciine and ponerine ants (partly owing to the wide adaptive radiation within the latter). By excluding some of the species having ergatoid queens, the following core profile of morphologically 'primitive' ants can be distilled out: (1) queens have low fecundity (1–5 eggs per day); (2) colonies consist of dozens or hundreds of workers; (3) predation is the rule; (4) solitary foraging predominates, but occasionally cooperation

and chemical recruitment have evolved. These characters contrast starkly with those of many 'higher' ants, i.e. hundreds of thousands of colony members, dramatic role specialization linked to worker polymorphism, and highly coordinated food-gathering strategies (e.g. *Dorylus*, *Atta*, *Oecophylla* or *Solenopsis*; see Hölldobler and Wilson 1990).

Some derived social traits can be exhibited by 'primitive' ants: (1) colonies can reach a few thousand workers, usually in species with ergatoid queens; (2) trophobiosis with homopterans and butterflies occurs in various ectatommine genera, together with pseudotrophallaxis among nestmates; (3) different degrees of group predation and migratory behavior are exhibited (e.g. in various species with ergatoids, including the amblyoponine *Onychomyrmex*). Nevertheless, other traits that are widespread in 'higher' ants are absent, i.e. no claustral colony foundation, no true trophallaxis (except in *Ponera coarctata* and *Hypoponera* sp.), and no worker polymorphism (except in *Megaponera*).

Limits on queen-worker dimorphism?

A consistent characteristic of morphologically 'primitive' ants is a generally limited divergence between winged queens and workers, and this represents the ancestral condition. Pronounced caste dimorphism occurs only in relatively few species with winged queens (e.g. *Paltothyreus*, *Paraponera*, a few *Pachycondyla*), as well as in several species with ergatoid queens (but this derived condition represents a distinct reproductive strategy, see below). Is there a restriction on the extent of reproductive specialization in 'primitive' queens? There is unlikely to be a structural limit on increasing thorax size, which would allow queens to have bigger wing muscles, and thus found colonies in complete isolation. Tergosternal fusion of abdominal segment IV (the sole apparent apomorphy of the Ponerinae) may be a morphological constraint on gaster enlargement (to accommodate bigger or more active ovaries), although expansion remains possible along the anteroposterior axis, i.e. intersegmental membranes can be stretched as in physogastric ergatoids of *Leptogenys*. Energetic constraints must also be considered: better-specialized queens are more expensive, and small colonies may not be able to produce them in adequate numbers (see below). Furthermore, since caste divergence affects colonial attributes (it is linked to queen fecundity, and thus colony size), the ecological consequences of increased divergence may or may not be selected for.

Small colony size and ecological specialization

Given the possibility of evolving higher queen fecundity, under what conditions is it adaptive for colonies to become more populous? Comparative data indicate that an increase in size alters the ecological profile of colonies markedly. More food needs to be found in the immediate environment to sustain additional larvae, which predatory species may not be able to achieve, even with a larger foraging force (prey density is finite). Furthermore, extra nest space needs to be available to accommodate the additional brood and adults. Wilson (1959) noted that limitation of nest space is an important factor in regulating colony size. For species with distinct requirements in the ground zone of forests (e.g. rotting log, natural cavities), enlargement of an existing nest may not be possible. Indeed, increased colony size means that nesting preferences need to be changed. In contrast, those ponerines that make ephemeral nests anywhere in litter, such as the legionary species, can have colonies with many workers.

Small colony size may thus be adaptive, and many 'primitive' species fill specialized ecological niches. They occur in low densities, and can coexist with ecologically dominant 'higher' ants. Further evidence that simple social traits can be selected for is their sporadic occurrence as secondary modifications in phylogenetically advanced species: (1) limited queen-worker differentiation in some formicines and formicoxenines; (2) small colonies in formicoxenines and various others; (3) solitary foraging and lack of chemical recruitment, e.g. in *Cataglyphis bicolor* (Wehner *et al.* 1983); (4) partly claustral mode of colony foundation, (5) absence of trophallaxis, e.g. two species of *Aphaenogaster* (Delage and Jaisson 1969).

Why is there no trophallaxis in 'primitive' ants? Three factors may act in concert: (1) the retrieval of insect prey makes the exchange of liquid food less appropriate; (2) tergo-sternal fusion of abdominal segment IV may be a constraint on considerable expansion of the crop; (3) in small colonies, food can be easily exchanged from foragers to the nestmates confined inside, and thus selection for trophallaxis is less strong. The lack of trophallaxis may partly explain why ponerine ants are almost absent from temperate regions. Because the internal storage of nutrients (as fat bodies) is not easily regulated, perennial colonies with carnivorous habits may not survive in regions where hunting is possible during a limited time of the year only. The complete exclusion of army ants (all predatory) from temperate regions supports this idea. Furthermore, ponerine spe-

cies with ephemeral nests above ground (e.g. rotten logs) would be unable to move deeply into the ground to escape low temperatures.

Evolution of derived reproductive strategies

Colony fission occurs throughout the ants, but is particularly common in 'primitive' taxa. This alternative to independent colony foundation is always exhibited in species having either ergatoid queens or gamergates, as well as in a few species with winged queens (see Peeters 1993).

Independent foundation vs. colony fission

A regular production of gynes is critical to the success of a queen-based breeding system. Colony resources must be allocated to produce a maximum number of gynes with a minimum number of workers (Hölldobler and Wilson 1990). Nuptial flight and mating are periods of high mortality for the young queens of many ants, no matter how highly specialized (Hölldobler and Wilson 1990). In species with large nest populations, individual colonies commonly release hundreds or thousands of winged gynes, and this large reproductive investment appears essential for the success of independent foundation.

Consequent to their limited morphological specialization, the winged queens of 'primitive' ants cannot establish new colonies without foraging. It is intuitive (although awaiting empirical verification) that this requirement leads to increased postdispersal mortality (predators, hostile workers from alien nests, or accidents). Nevertheless, the persistence of semiclastral foundation in many extant *Myrmecia* spp. and Ponerinae is evidence of its viability under certain ecological conditions. Species having more dimorphic castes may exhibit a higher success rate during colony foundation, or this success may be due to favorable local factors (e.g. assembly of ant competitors). Alternatively, the reproductive investment of some species can be large enough to compensate for high foundress mortality. In *Paltothyreus tarsatus*, several hundreds of specialized big gynes can be reared in colonies having one or more thousands of workers (Braun *et al.* 1994b). Various benefits of dispersal by flight (increased genetic diversity, reduction in local competition, colonization of new habitats) are certainly also involved.

Small colony size restricts the amount of resources that can be invested annually in the production of sexuals. Some species may be unable to produce a sufficiently

large number of new gynes, and independent foundation is then selected against (Peeters 1990). Once fission occurs instead, aerial dispersal by queens stops, and mating strategy changes (Peeters 1991a). Thus the continued production of winged female reproductives stops being adaptive (see Tinaut and Heinze 1992). Ergatoid queens may have evolved as a consequence, while in other species gamergates replaced the queen caste.

Ergatoid queens and high fecundity

Because ergatoid queens are accompanied by workers during colony fission, their rate of success is likely to increase greatly (no need to forage, and sometimes they even mate with foreign males inside the nests). Furthermore, since an existing colony can only divide into two (three at the most) viable buds at one time, there will be selection to reduce the number of new queens produced (see Franks and Hölldobler 1987). Thus only a few ergatoids are reared annually, and available colony resources can be used to produce more workers. Indeed, the number of workers determines the viability of daughter colonies, and they represent most of the reproductive investment (Macevitz 1979). This pattern has been well documented in army ants, but empirical data remain scarce in the Ponerinae and *Myrmecia*.

In ant queens generally, morphological specialization serves two distinct functions: (1) dispersal and colony foundation, i.e. large flight muscles, and stored metabolic reserves to produce the first brood of workers; (2) high rate of egg production, i.e. bigger ovaries (more ovarioles, or longer ovarioles) as well as smaller eggs (so that more oocytes can mature simultaneously). The evolution of ergatoid queens clearly reveals that components (1) and (2) can be modified independently. Ergatoids have a worker-like thorax and are incapable of founding colonies independently, but they are highly fecund in various ponerine species where an increase in colony size is adaptive. In other species with ergatoid queens, ovarian specialization remains limited, and colonies are not larger than in species with winged queens. Accordingly, the ecological characteristics of 'primitive' species with ergatoids are extremely varied.

The gamergate strategy is cheap

In queenless species, those workers that do not differentiate as gamergates function as laborers, and consequently reproductive investment (which is equal to worker production, as in species with ergatoid queens) is optimized.

Gamergates have a relatively short lifespan, but they can be replaced in colonies without too many risks to colony survival.

The ecological profiles of species with gamergates are often similar, despite belonging to different tribes and genera. They tend to be solitary foragers without strict prey preferences, and often but not always are found in drier environments. However such combination of traits are also exhibited by various queenright ponerines. More comparative data are needed to derive a complete explanation for the absence of the queen caste in a small number of ants. Future studies of microhabitat preferences, including seasonal shortages in prey availability (trophic shortages may coincide with the period of sexual production, especially since internal storage of nutrients is impossible), may help our understanding of the ecological conditions under which queen reproduction was selected against. Investigation of species in which both queens and gamergates reproduce (Table 18-1) will yield valuable insights into their respective abilities (e.g. *Harpegnathos saltator*, Peeters and Hölldobler 1995).

Future perspectives

Tschinkel (1991) has advocated the systematic collection of descriptive data on the colony attributes of social insects, in order to determine the relationships among these attributes, both at an intraspecific and comparative level. Such sociometric data are badly needed for a large number of morphologically 'primitive' ants (*Myrmecia* in particular), for example, colony size, queen fecundity, queen and worker longevity. Although some of these data are best collected in the laboratory, other data must originate from the field, such as the mortality rate of queens during independent colony foundation, the importance of predators and parasitoids, the number of sexuals produced annually (especially ergatoid queens), and mechanisms of colony fission. Reliable phylogenies are also needed to determine which characters are ancestral or derived.

Specialization of queen morphology is a key to social complexity. The 'primitive' ants exhibit the early stages of the evolutionary divergence between reproductive and helper castes, and thus offer the opportunity to investigate the selective pressures responsible for increased sophistication of colony organization. The occurrence of three distinct reproductive strategies (sometimes in the same genus) is of particular comparative interest.

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