

Convergent evolution of wingless reproductives across all subfamilies of ants, and sporadic loss of winged queens (Hymenoptera: Formicidae)

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Abstract

Flight is a one-off event in ants, hence after mating, the wing muscles of winged queens can function as protein reserves during independent colony foundation (ICF). Another strategy occurring in many unrelated lineages is dependent colony foundation (DCF). DCF does not require queens with expensive wing muscles because dispersal is on foot, and a foundress relies on nestmate workers to feed her first brood of workers. The shift to DCF seems the reason why wingless reproductives (ergatoid queens, short-winged queens, and gamergates) evolved independently in more than 50 genera belonging to 16 subfamilies. In various species they occur together with winged queens (in the same or different populations), in other species winged queens were replaced completely. Because wingless reproductives are the product of convergence, there is tremendous heterogeneity in morphological characteristics as well as selective contexts. These novel reproductive phenotypes cannot function without nestmate workers (foundresses forage in only few species), hence additional investment in workers is needed.

Key words: Colony foundation, flight, reproduction, dispersal, brachyptery, ergatoid queens, gamergates, review.

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Introduction

In the ants, flight is restricted to a brief dispersal phase involving young queens and males. Once mated, queens shed their wings. This and the winglessness of workers are adaptations for ground-living, as in termites. In sharp contrast are social wasps and bees where flight remains essential for all activities, both in queens and workers. In ants, the flight apparatus of queens has an additional function after mating. During independent colony foundation (ICF), queens can break down their wing muscles, freeing up amino acids to feed the first generation of workers. In many species the wing muscles are large enough to raise the first offspring without any outside nourishment (i.e., ICF is claustral). Hence ant queens can be highly specialized for ICF; metabolic reserves are less important in termites where founding pairs can feed on cellulose available in the confines of the nest.

Social insects have an alternative strategy of colony foundation whereby the queen is not alone, so called dependent colony foundation (DCF). The foundress(es) is continuously helped by nestmate workers who shield her from all risks during dispersal and feed her offspring in the new nest. DCF is likely to be associated with a dramatic decrease in the mortality of foundresses. In the ants, DCF (which includes a variety of behaviours encompassing "fission" and "budding") leads to a sharp drop in female dispersal range since queens must travel on foot with the workers (PEETERS & MOLET 2009). Accordingly flying abi-

lity is no longer selected for, and the second function of wing muscles as metabolic reserves stops being adaptive because it is the workers that obtain food for the queen's brood.

The existence of wingless reproductives in ants was reported more than a century ago (e.g., FOREL 1895). WHEELER (1917) described "ergatoid queens" with a simplified thorax (a consequence of lacking wing muscles) resembling that of workers (see Box 1). Together with short-winged "brachypterous" queens that cannot fly, ergatoid queens have been found in an increasing number of species (e.g., PEETERS 1991, BUSCHINGER & HEINZE 1992, TINAUT & HEINZE 1992, HEINZE & TSUJI 1995, PEETERS & ITO 2001). Another type of wingless reproductives are the "gamergates" (mated egg-laying workers) of species in which all members of the worker caste have a functional spermatheca (GOBIN & al. 2008). Here I survey the literature to determine the distribution of ergatoid queens, brachypterous queens, and gamergates across all lineages of ants. In many species, they occur as well as winged queens. In many other species, winged queens have disappeared completely. I discuss that wingless reproductives are novel phenotypes that uncouple flight and sexual reproduction. I argue that the selective pressures causing the replacement of winged queens are linked to a trade-off between different founding strategies: Successful ICF requires many expensive winged gynes (i.e., young queens), but DCF requires fewer and cheaper wingless gynes together with many workers.

Box 1: What are "ergatoid queens"? A recent history of the terminology concerning permanently wingless reproductives in ants.

The term "ergatoid" means "worker-like" and is confined to the ant (and termite) literature. As far back as FOREL (1895) and EMERY (1895), the simplified morphology of ant workers was taken as a benchmark to compare other wingless castes as well as wingless males. The lack of wings and flight muscles leads to a fusion of thoracic sclerites: 43 sclerites in winged queens are reduced to 4 - 12 in workers (R.A. Keller, pers. comm.). Across lineages, queens that emerge without wings vary greatly in the extent of their similarity to the worker caste; in some species they retain some flight sclerites and resemble more the thorax of winged queens. BOLTON (1986) distinguished between "apterous queens" and "extreme ergatoids" in the *Monomorium salomonis*-group, depending on different degrees of thorax simplification. In *Acanthomyrmex*, EGUCHI & al. (2008) used "dwarf queens" for wingless queens with distinct flight sclerites (and a smaller thorax), but "ergatoid queens" in other species where the thoracic sclerites are fused. There has been a similar reluctance to use "ergatoid queens" in dorylomorph species (army ants) where apterous queens have a greatly expanded gaster and hence do not resemble workers; these are traditionally termed "dichthadiiform".

PEETERS (1991) was mistaken to make a distinction between ergatoid queens and "reproductive intercastes" as found in some formicoxenine species. The latter are morphologically variable within colonies, and they can coexist with winged queens. HEINZE (1998) rightly considered that since "reproductive intercastes" occur regularly and have a definite function, they are entirely different from erratically produced anomalies, which may or may not have a spermatheca (PEETERS 1991). I concur with HEINZE (1998) that "intercastes" must be restricted to anomalous intermediates between winged queens and workers.

As more species come under scrutiny, it becomes clear that the morphology of permanently wingless queens can be either fixed or variable, and distinct categories are not heuristic. Moreover, whether they replace winged queens completely is a separate issue. I advocate the use of "ergatoid queens" for all wingless reproductives that differ morphologically from workers; this difference can be as little as the occurrence of a spermatheca (see MOLET & al. 2009). Terms like "intermorphic queens" ("morphologically variable female reproductives which more or less resemble normal workers externally", e.g., HEINZE & BUSCHINGER 1987), "dwarf queens" and "dichthadiiform" seem superfluous to me.

Wing muscles in ant queens are an adaptation for independent colony founding

Many "formicoid" species (90% of all ants; WARD 2007) have evolved winged queens with disproportionately huge wing muscles compared to any normal flying wasps (Fig. 1). This seems an adaptation for claustral ICF, not better flying: The enlarged thorax muscles can store enough proteins to rear the first generation of workers without foraging outside. In addition, fat stores and storage proteins are accumulated prior to dispersal (PASSERA & KELLER 1990, WHEELER & BUCK 1995, 1996). The importance of these metabolic reserves is amplified by the large size dimorphism between queen and worker castes in numerous formicoids: Workers can be minute, reaching one millimetre, hence many can be quickly produced in the first brood.

In contrast, the queens of phylogenetically basal (i.e., retaining many ancestral traits) "poneroid" species are generally similar in size to conspecific workers, and their flight thorax is only slightly bigger (Fig. 2). The wing muscles are also broken down during ICF, but foundresses need to hunt insects above ground, i.e., ICF is non-claustral (HASKINS & HASKINS 1955, PEETERS 1997). Foraging by founding queens also evolved secondarily in some formicoid species (BROWN & BONHOEFFER 2003). Foraging outside the incipient nest exposes foundresses to predators and accidents, and the undefended brood can suffer from parasites. Hence claustral ICF is a major adaptation since foundresses remain in the relative safety of a sealed chamber. It is intuitive that their mortality rate is considerably decreased (see PEETERS & MOLET 2009).

An alternative strategy of claustral ICF is parasitism, either intra- or inter-specific. Instead of accumulating reserves, lone foundresses exploit established ant colonies as an environmental resource (PEETERS & MOLET 2009). Dispersing queens are not helped by nestmate workers, supporting the notion that parasitism is akin to ICF, not DCF.

Wing muscles of insects cost substantially to develop and maintain, with up to 65% of total body mass and a metabolic rate nine times higher than for ovarian tissue (Marden 2000). In ants, this large cost is offset by their second function: amino acid reserves during ICF. Unfortunately, detailed data comparing poneroid and formicoid queens are not available, although thorax volume gives a good approximation. It is evident that the annual production of gynes with a big thorax is a huge investment for ant colonies.

In conclusion, the phenotype of winged queens is generally characterized as a bigger thorax (relative to workers) coupled with a bigger gaster. This corresponds to two crucial adaptations: aerial dispersal together with ICF, and increased ovarian development underlying high fecundity. In addition, substantial size differences often evolved between the castes.

Recurrent evolution of dependent colony foundation

DCF has evolved from ICF in many distantly related lineages of social Hymenoptera. DCF is a dramatically different strategy: Founding queens no longer behave like solitary insects. They disperse together with nestmate workers, and they do not provide food for their offspring. Dispersal carries fewer risks because the workers can go to a pre-

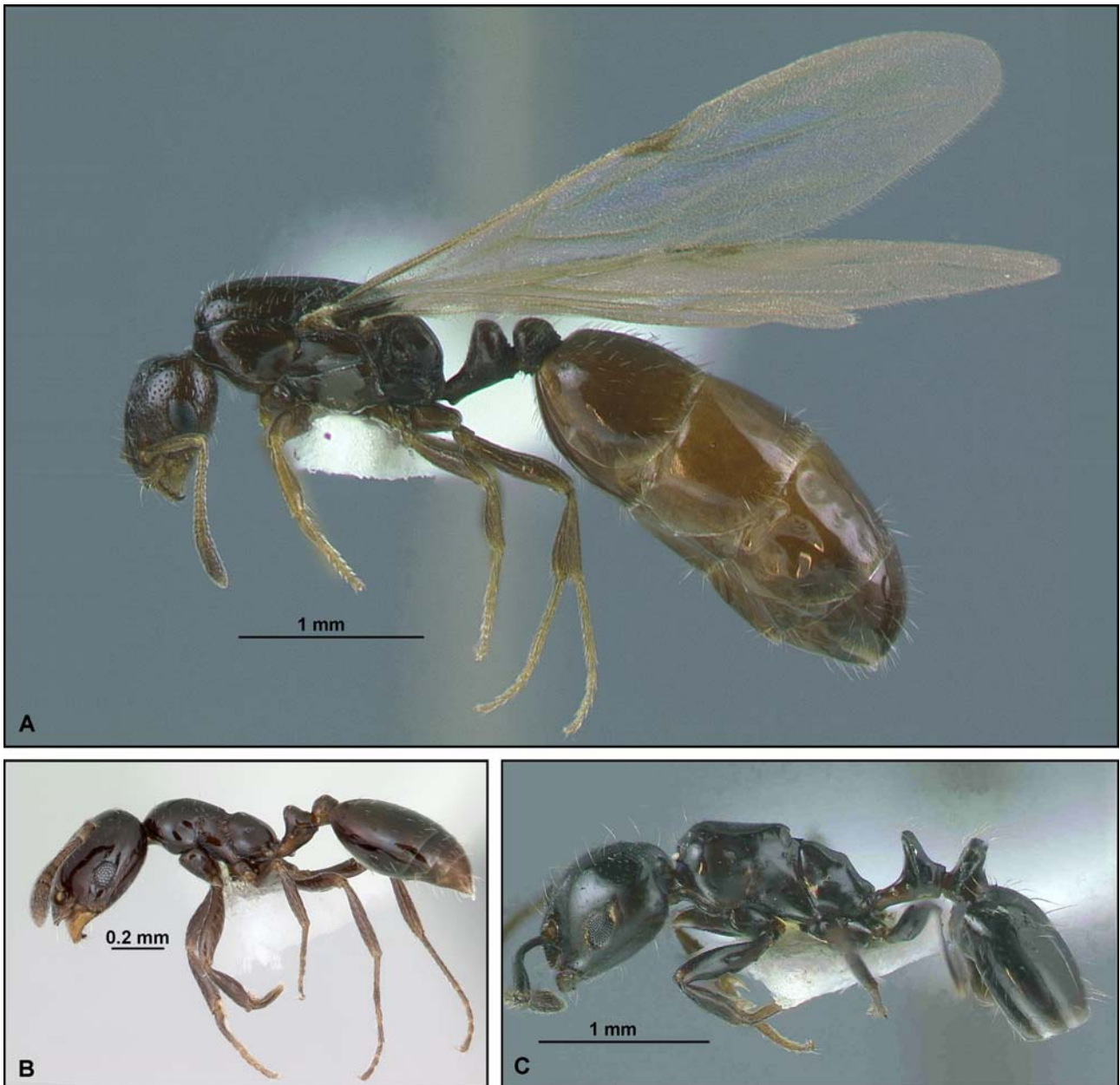


Fig. 1: (A) Winged queen and (B) worker of the formicoid *Monomorium minimum*-group, showing big size dimorphism. (C) Ergatoid queen of *M. algericum* (gaster partly dissected: 30 - 40 ovarioles) is added for comparison. © antweb.org (A + B), © C. Peeters (C).

viously located nesting site. New colonies start with a substantial number of helpers, thus buffering against food shortages, improving competition with established colonies, and allowing the rapid production of sexuals (ants reviewed in PEETERS & MOLET 2009).

There is neither theoretical reason nor empirical evidence that DCF is less costly for the mother colony compared to ICF. The shift to DCF requires important changes in reproductive investment because the worker force determines the success of incipient colonies. Nestmates need to be sufficiently numerous to allow colonies to divide into two or more parts. The increased investment in workers is compensated by producing fewer gynes. Fewer are needed because they have a much lower mortality rate. Moreover, since existing colonies divide into a finite number of daughter colonies, gynes reared in excess cannot succeed.

Unlike social wasps and bees, DCF ants can improve colonial economy by changing the physiology or morphology of reproductives. There is no longer selective pressures on a flying phenotype, and expensive winged gynes are not required. However, wingless reproductives cannot be considered in isolation from nestmate workers, which can be viewed as the extended body of such reproductives. Workers are less costly and function more flexibly than queens, and the increased interdependency between castes represents a novel solution uniquely suited to social life.

Wingless reproductives occur in all major ant sub-families

Table 1 lists 77 genera in which at least one species has wingless reproductives (i.e., ergatoid queens, brachypterous queens, or gamergates). These genera belong to 16 subfam-

Tab. 1: Ant genera (77 out of a total of 295, BOLTON 2011) with ergatoid queens (EQ), short-winged queens (BQ) or gamergates (G) known from functional evidence, or deductions from external morphology, or both. Some species have only wingless reproductives; in others these occur as well as winged queens (AQ). * indicates genera in which AQ are completely unknown. Five monotypic subfamilies are not listed because they have AQ only, or queens have not been collected.

Subfamily (total number of genera)	Genus (total number of species)	One exemplar species having wingless reproductives (morph)	References
Amblyoponinae (11)	<i>Adetomyrma</i> (1)	"mg02" (EQ)	www.antweb.org
	<i>Amblyopone</i> (72)	<i>reclinata</i> gr. (G)	ITO (1993)
	<i>Mystrium</i> (10)	<i>oberthueri</i> (EQ)	MOLET & al. (2009)
	<i>Onychomyrmex</i> (3) *	<i>hedleyi</i> (EQ)	MIYATA & al. (2003)
Ponerinae (27)	<i>Platythyrea</i> (38)	<i>conradti</i> (EQ) <i>lamellosa</i> (G) <i>quadridenta</i> (AQ + G)	MOLET & PEETERS (2006) VILLET & al. (1990) ITO (1994)
	<i>Anochetus</i> (94)	<i>kempfi</i> (EQ)	TORRES & al. (2000)
	<i>Diacamma</i> (24) *	<i>australe</i> (G)	PEETERS & HIGASHI (1989)
	<i>Dinoponera</i> (6) *	<i>quadriceps</i> (G)	MONNIN & PEETERS (1998)
	<i>Dolioponera</i> (1) *	<i>fustigera</i> (EQ)	FISHER (2006)
	<i>Harpegnathos</i> (7)	<i>saltator</i> (AQ + G)	PEETERS & al. (2000)
	<i>Hypoponera</i> (126)	<i>bondroiti</i> (AQ + EQ)	YAMAUCHI & al. (1996)
	<i>Leptogenys</i> (216)	<i>diminuta</i> (EQ) <i>peuqueti</i> (G)	MASCHWITZ & al. (1989) ITO (1997)
	<i>Myopias</i> (34)	<i>concava</i> (AQ + EQ)	WILLEY & BROWN (1983)
	<i>Odontomachus</i> (62)	<i>coquereli</i> (EQ)	MOLET & al. (2007)
	<i>Pachycondyla</i> (252)	<i>analisis</i> (EQ) <i>berthoudi</i> (G) <i>tridentata</i> (AQ + G)	VILLET (1990) PEETERS & CREWE (1985) SOMMER & al. (1994)
	<i>Plectroctena</i> (16)	<i>mandibularis</i> (EQ)	VILLET (1991)
	<i>Simopelta</i> (21) *	<i>oculata</i> (EQ)	GOTWALD & BROWN (1966)
	<i>Streblognathus</i> (2) *	<i>peetersi</i> (G)	CUVILLIER-HOT & al. (2004)
	<i>Thaumatomyrmex</i> (12)	<i>atrox</i> (G)	JAHINY & al. (2002)
Proceratiinae (3)	<i>Discothyrea</i> (32)	some species (EQ)	BROWN (1958: p. 251)
	<i>Probolomyrmex</i> (20)	<i>guanacastensis</i> (EQ)	O'KEEFE & AGOSTI (1997)
	<i>Proceratium</i> (78)	"mg03" (EQ)	C. Peeters & B.L. Fisher, unpubl.
Leptanillinae (5)	<i>Leptanilla</i> (43) *	<i>japonica</i> (EQ)	MASUKO (1990)
Aenictinae (1)	<i>Aenictus</i> (133) *	<i>eugenii</i> (EQ)	GOTWALD & CUNNINGHAM-VAN SOMEREN (1976)
Cerapachyinae (5)	<i>Acanthostichus</i> (22) *	all species (EQ)	BROWN (1975: p. 40)
	<i>Cerapachys</i> (146)	<i>antennatus</i> (EQ)	BROWN (1975: p. 59)
	<i>Simopone</i> (17)	<i>emeryi</i> (EQ)	B.L. Fisher, unpubl.
	<i>Sphinctomyrmex</i> (22)	<i>steinheili</i> (EQ)	BROWN (1975: p. 31)
Dorylinae (1)	<i>Dorylus</i> (59) *	<i>gribodoi</i> (EQ)	SCHÖNING & al. (2008)
Ecitoninae (5)	<i>Eciton</i> (12) *	<i>sumichrasti</i> (EQ)	WHEELER (1900)
	<i>Labidus</i> (7) *	<i>coecus</i> (EQ)	WEBER (1941)
	<i>Neivamyrmex</i> (124) *	<i>moseri</i> (EQ)	WATKINS (1971)
	<i>Nomamyrmex</i> (2) *	<i>esenbeckii</i> (EQ)	BORGMEIER (1958)
Leptanilloidinae (3)	<i>Leptanilloides</i> (8) *	<i>nubecula</i> (EQ)	DONOSO & al. (2006)
Ectatomminae (4)	<i>Gnamptogenys</i> (137)	<i>menadensis</i> (AQ + G)	GOBIN & al. (1998)
	<i>Rhytidoponera</i> (104)	<i>confusa</i> (AQ + G) <i>mayri</i> (G)	WARD (1983) PEETERS (1987)
	<i>Typhlomyrmex</i> (7)	sp.4 (AQ + EQ)	LACAU (2005)

Heteroponerinae (2)	<i>Heteroponera</i> (17)	<i>relicta</i> (EQ)	PEETERS (1991) WHEELER (1915)
Myrmeciinae (2)	<i>Myrmecia</i> (89)	<i>pulchra</i> (EQ) <i>regularis</i> (BQ)	CLARK (1951) HASKINS & HASKINS (1955)
	<i>Nothomyrmecia</i> (1) *	<i>macrops</i> (BQ)	TAYLOR (1978)
Pseudomyrmecinae (3)	<i>Tetraoponera</i> (89)	<i>tessmanni</i> (BQ)	DJIÉTO-LORDON & al. (2005)
Dolichoderinae (28)	<i>Aptinoma</i> (2)	<i>mangabe</i> (EQ)	FISHER (2009)
	<i>Dolichoderus</i> (122)	<i>cuspidatus</i> (EQ)	MASCHWITZ & HÄNEL (1985)
	<i>Leptomyrmech</i> (27)	<i>nigriventris</i> (EQ)	WHEELER (1934)
	<i>Tapinoma</i> (62)	<i>littorale</i> (BQ)	J. Heinze, pers. comm.
	<i>Technomyrmex</i> (92)	<i>brunneus</i> (AQ + EQ)	TSUJI & al. (1991)
Formicinae (49)	<i>Cataglyphis</i> (85)	<i>velox</i> (BQ)	TINAUT & HEINZE (1992)
	<i>Formica</i> (176)	<i>subrufa</i> (BQ)	TINAUT & RUANO (1992)
	<i>Lasius</i> (99)	<i>crypticus</i> (AQ + BQ)	S. Cover, pers. comm.
	<i>Plagiolepis</i> (57)	<i>maura</i> (EQ)	ESPADALER (2007)
	<i>Polyergus</i> (5)	<i>samurai</i> (AQ + EQ)	TERAYAMA & al. (1993)
	<i>Polyrhachis</i> (614)	<i>robsoni</i> (AQ + BQ)	HEINZE & HÖLLDOBLER (1993)
	<i>Proformica</i> (25)	<i>longiseta</i> (BQ)	FERNANDEZ & al. (2001)
Myrmicinae (141)	<i>Acanthomyrmex</i> (17)	<i>glabfemoralis</i> (AQ + EQ) <i>padanensis</i> (EQ)	EGUCHI & al. (2008) TERAYAMA & al. (1998)
	<i>Aphaenogaster</i> (175)	<i>araneoides</i> (EQ) <i>senilis</i> (BQ)	LONGINO & COVER (2004) TINAUT & RUANO (1992)
	<i>Blepharidatta</i> (2) *	<i>conops</i> (EQ)	BRANDÃO & al. (2001)
	<i>Calyptomyrmex</i> (25)	<i>piripilis</i> (EQ)	BOLTON (1981: p. 65)
	<i>Cardiocondyla</i> (67)	<i>batesii</i> (AQ + BQ)	HEINZE & al. (2002)
	<i>Eutetramorium</i> (2)	<i>mocquerysi</i> (EQ)	HEINZE & al. (1999)
	<i>Formicoxenus</i> (7)	<i>nitidulus</i> (AQ + EQ)	FRANCOEUR & al. (1985)
	<i>Harpagoxenus</i> (3)	<i>sublaevis</i> (AQ + EQ)	BUSCHINGER & WINTER (1975)
	<i>Hylomyrma</i> (13)	<i>immanis</i> (EQ)	KEMPF (1973)
	<i>Leptothorax</i> (18)	sp. A (AQ + EQ)	HEINZE & BUSCHINGER (1987)
	<i>Lordomyrma</i> (27)	unspecified (EQ)	BOLTON (2003)
	<i>Manica</i> (6)	<i>rubida</i> (AQ + BQ)	LENOIR & al. (2010)
	<i>Megalomyrmex</i> (37)	<i>goeldii</i> (AQ + EQ) <i>leoninus</i> gr. (EQ)	BRANDÃO (1990) BRANDÃO (1990)
	<i>Metapone</i> (18)	<i>madagascarica</i> (AQ + G)	HÖLLDOBLER & al. (2002)
	<i>Monomorium</i> (385)	<i>hesperium</i> (EQ) <i>leae</i> (AQ + EQ)	BOLTON (1986) FERSCH & al. (2000)
	<i>Myrmecina</i> (51)	sp. A (EQ) <i>nipponica</i> (AQ + EQ)	ITO (1996) OHKAWARA & al. (1993)
	<i>Octostruma</i> (13)	<i>rugifera</i> (AQ + EQ)	BROWN & KEMPF (1960)
	<i>Ocymyrmex</i> (37) *	<i>picardi</i> (EQ)	BOLTON & MARSH (1989)
	<i>Pogonomyrmex</i> (67)	<i>huachucanus</i> (BQ) <i>pima</i> (AQ + EQ)	JOHNSON (2010) JOHNSON & al. (2007)
	<i>Pristomyrmex</i> (57)	<i>africanus</i> (AQ + EQ) <i>mandibularis</i> (EQ)	WANG (2003) WANG (2003)
	<i>Stereomyrmex</i> (3)	<i>horni</i> (EQ)	BOLTON (2003: p. 273)
	<i>Temnothorax</i> (335)	<i>kinomurai</i> (EQ)	TERAYAMA & ONOYAMA (1999)
	<i>Terataner</i> (12)	<i>foreli</i> (EQ)	ALPERT (1992)
	<i>Vollenhovia</i> (58)	<i>emeryi</i> (AQ + BQ) <i>yambaru</i> (EQ)	OHKAWARA & al. (2006) TERAYAMA (1999)

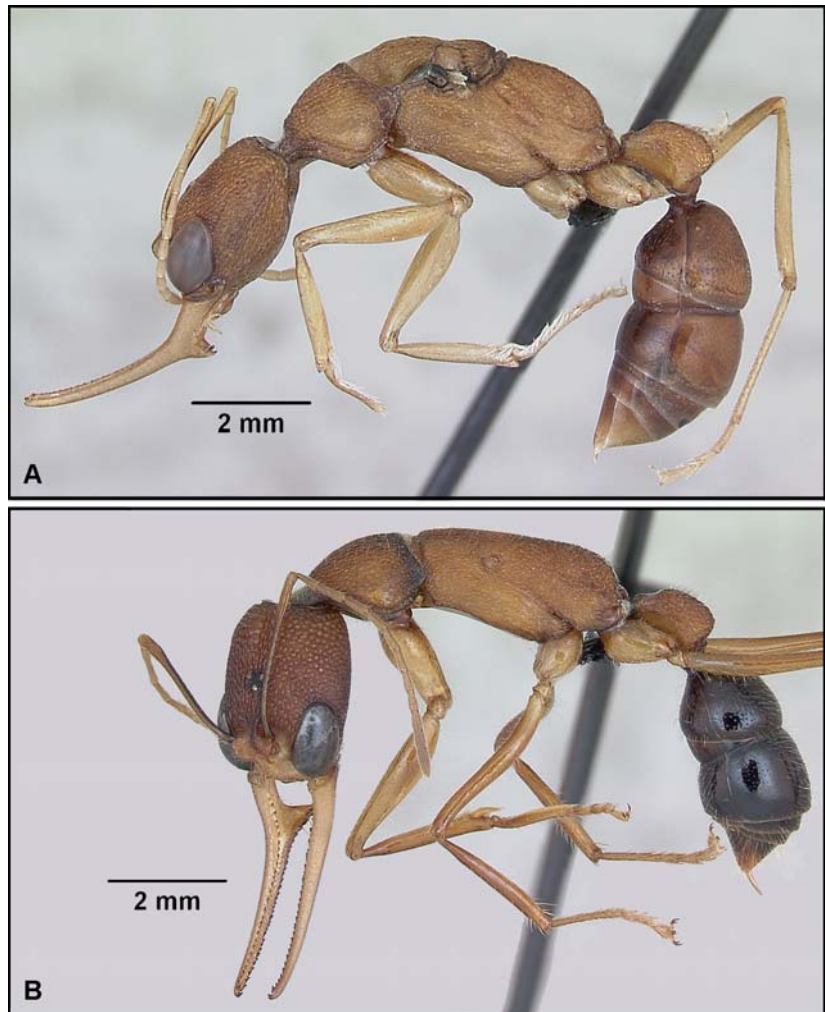


Fig. 2: (A) Winged queen (dealate) and (B) worker of the poneroid *Harpegnathos saltator*, showing very limited size dimorphism. Both castes have six ovarioles. © antweb.org

ilies, including all major ones, out of a total of 21. These comparative data indicate that wingless reproductives have independently evolved in lineages having winged queens. A proportion of species with wingless reproductives also have winged queens, but others lack them completely. Species that have two morphs of reproductives (e.g., AQ [winged queens] + G [gamergates], AQ + EQ [ergatoid queens]; Tab. 1) give us the opportunity to compare their morphological and functional differences (e.g., OHKAWARA & al. 1993, PEETERS & al. 2000). Alternatively, congeneric species differing in reproductive morphs can be studied, but for large genera a species-level phylogeny is needed to recognize appropriate comparisons.

(1) Ergatoid queens

These reproduce in 55 genera across 15 subfamilies (Tab. 1), meaning they evolved again and again. The term "ergatoid" (worker-like) refers to their simplified thorax which gives them the appearance of workers (Box 1). Wing muscles are absent, causing a more or less important fusion of the original flight sclerites, although the thorax almost always remains distinct from workers'. In a majority of species, ergatoid queens have a bigger gaster than workers, and they often have more ovarioles. Importantly, they always have a spermatheca to store sperm, unlike conspecific workers; exceptions are *Cerapachys biroi* (see RAVARY & JAIS-

SON 2004) and *Pristomyrmex punctatus* (see ITOW & al. 1984, TSUJI & DOBATA 2011) because both ergatoid queens and workers reproduce parthenogenetically. Ergatoid queens often have allometric relationships between body parts that differ from workers' (e.g., MOLET & al. 2007, 2009). Across species, they have more or less vestigial ocelli, i.e., reduced in size, number or pigmentation, and absence of a corneal lens. In insects, ocelli are light meters involved in stabilization reflexes during flight (KRAPP 2009); they are lost in non-flying insects (e.g., ant workers, with some exceptions). Similarly, the ocelli in ergatoid queens are non-functional but may provide insights about developmental pathways (i.e., relative to winged queens).

Winged queens across the ants are a caste defined by uniform morphology as well as shared ancestry. During the adaptive radiation of ants, the degree of queen-worker dimorphism changed considerably, but the basic characteristics of a flying insect (especially the strong constraints on thorax structure) remained unchanged. In contrast, ergatoid queens result from multiple convergent evolution events. They group together as one broad category ("reproductive caste lacking wings but morphologically distinct from workers"), although they lack shared ancestry. Across lineages, the characteristics of ergatoid queens vary considerably – in terms of thoracic simplification, overall reduction in size, and general biology. Among closely related species (e.g.,

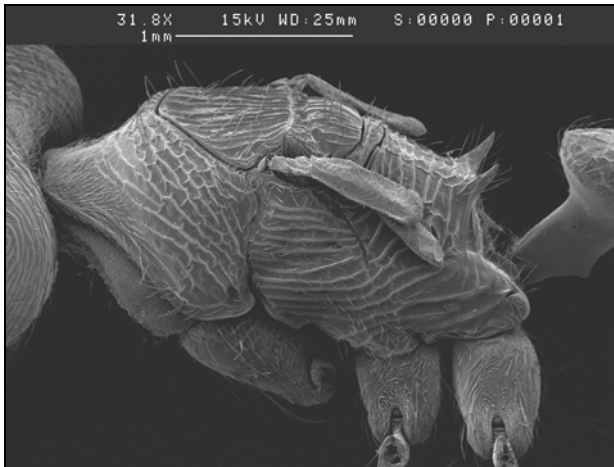


Fig. 3: Scanning electron micrograph of the thorax of a brachypterous queen of *Pogonomyrmex laticeps*. Note the flight sclerites are not fused. © C. Peeters.

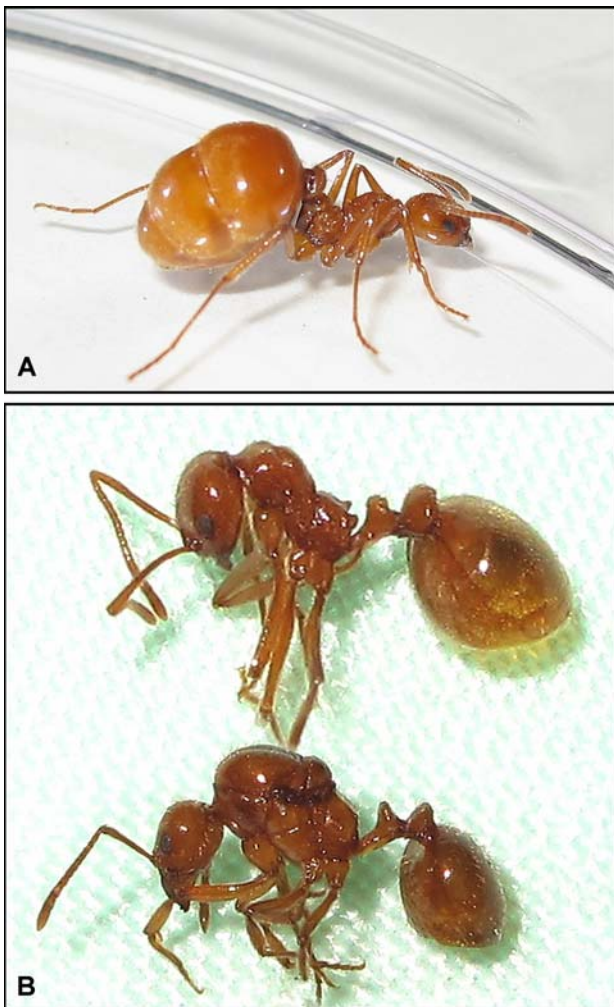


Fig. 4: (A) Ergatoid queen of *Megalomyrmex foreli* showing her large gaster. (B) Ergatoid queen of *M. foreli* compared to a dealate queen of *M. modestus*, highlighting the dissociation between thorax and gaster size. Both queens were dissected (60 - 70 and 24 - 28 ovarioles, respectively) and only the first segment of gaster is seen. © C. Peeters.

Monomorium salomonis-group, BOLTON 1986), ergatoid queens can show different degrees of fusion of the flight sclerites. Ergatoid queens can be much bigger than conspecific workers (e.g., dorylomorphs, *Monomorium*, *Onychomyrmex*), moderately size-dimorphic (e.g., *Acanthomyrmex*, *Heteroponera*, *Plectroctena*), or very similar in size to workers (e.g., *Eutetramorium mocquerysi*, *Ocymyrmex*, *Proceratium*, *Terataner*). In the latter, the key difference between castes is presence of a spermatheca. In a few species that retain winged queens ("AQ + EQ" in Tab. 1), the external morphology of ergatoid queens varies within colonies. In *Technomyrmex brunneus* the smallest ergatoid queens lack any ocelli and have similar body sizes to workers; their ovariole number is intermediate between larger ergatoid queens and workers, but all can mate and store sperm (TSUJI & al. 1991). In *Myrmecina nipponica*, ergatoid queens exhibit different degrees of thoracic simplification; ovariole number is constant but spermatheca size varies, and individuals at the lower end cannot mate (OHKAWARA & al. 1993). In *Sphinctomyrmex* cf. *steinheili*, ergatoid queens vary in size and ovariole numbers; several are mated and reproduce in the same colonies (BROWN 1975, BUSCHINGER & al. 1989).

Various species of *Crematogaster* (*Orthocrema* subgenus) have wingless females that are intermediate in size between winged queens and workers, and they have more ovarioles than workers; they lay eggs but lack a spermatheca (HEINZE & al. 1999; C. Peeters & J. Billen, unpubl.). Such a caste has a trophic function, they cannot reproduce sexually and are not ergatoid queens.

(2) Brachypterous queens

Short-winged queens are comparable to ergatoid queens. They are clearly unable to fly and generally lack wing muscles (e.g., *Cardiocondyla*, see SCHREMPF & HEINZE 2007; R. Keller, pers. comm.). Their wings range from two-thirds the normal length to very small, and these are often shed soon after pupal emergence. Their thorax is often less simplified than that of ergatoid queens, and is thus conspicuously distinct from workers' (Fig. 3). Once dealated, brachypterous queens are easily mistaken (e.g., in museum collections) for normal winged queens. They can also be confused for ergatoid queens in species where the tiny vestigial wings are quickly removed after emergence (e.g., *Cerapachys* mg02, C. Peeters, unpubl.). Brachypterous queens are currently known in 14 genera but are probably more widespread (Tab. 1). They are unknown in poneroid subfamilies.

In *Aphaenogaster*, *Monomorium*, *Myrmecia*, and *Pogonomyrmex*, congeneric species have either ergatoid or brachypterous queens (Tab. 1 & BRIESE 1983), suggesting that these are alternative solutions to obviate the costs of the flight apparatus. Ergatoid and brachypterous queens are found in different populations of *Pogonomyrmex laticeps* (C. Peeters, R. Keller & R. Johnson, unpubl.), while both are produced in the same colonies of *Cataglyphis floricola* (see AMOR & al. 2011).

(3) Gamergates

Mated workers reproduce in 11 genera (from three subfamilies), three of which completely lack winged queens (Tab. 1). A molecular phylogeny shows that the genus *Pachycondyla* (167 species) consists of over ten monophyletic clades (SCHMIDT 2009), indicating a minimum of five

independent evolution of gamergate reproduction (C. Schmidt & C. Peeters, unpubl.). Gamergates have also been reported in laboratory colonies of *Metapone* (see HÖLLDOBLER & al. 2002) and *Myrmecia* (see DIETEMANN & al. 2004), but further study is needed to assess their natural occurrence. Since gamergates are morphologically the same as infertile workers, they are fully distinct from ergatoid queens.

Ergatoid and brachypterous queens uncouple flight and reproduction

Wingless reproductives contrast morphologically and behaviourally with ancestral winged queens because they uncouple (1) ability to disperse by flight and found colonies independently, and (2) ability to mate and reproduce sexually. Many solitary insects have both winged and wingless morphs, but the latter just differ in the presence of wing muscles and the size of wings (ROFF 1990). In ants however, the external morphology of ergatoid and brachypterous queens is highly discrete from closely related winged queens. They are often smaller than winged queens except for the gaster (Fig. 4). Importantly, they cannot survive alone (unlike dealate foundresses) and need the help of nestmate workers during all stages of colony foundation. Hence, wingless reproductives cannot be thought of as queens simply lacking wings (e.g., BUSCHINGER & HEINZE 1992). I argue that ergatoid and brachypterous queens are novel phenotypes in which thorax and gaster morphology are dissociated.

(1) Loss of flight restricts mating behaviour

Two syndromes are used to describe the continuum of male and gyne behaviours across ant species (HÖLLDOBLER & BARTZ 1985): "female calling" (solitary gynes wait for foreign males near their natal nest) and "male aggregations" (gynes and males from many colonies fly to one common spot; mated gynes then fly further). All wingless reproductives exhibit female calling, which occurs outside or inside their nest. It is likely that males use their exceptionally large eyes to locate single females on the ground, while sexual pheromones function to recognize sexual partners at closer range. Some ponerine males can locate conspecific nests by following the recruitment trails of workers (PEETERS 1997).

Female calling seems the ancestral pattern in ants, and it is a widespread behaviour for winged gynes of poneroid clades (PEETERS & MOLET 2009). Female calling does not exclude aerial dispersal and ICF, which can occur after copulation, e.g., in *Cardiocondyla* (see SEIFERT 2003), *Rossomyrmex minuchae* (see RUANO & TINAUT 2005). However, in other species, the winged gynes mate outside their natal nest and then re-enter (sometimes termed "adoption"). They can either engage in DCF with nestmate workers, or otherwise they function as secondary reproductives. Similarly, female calling by wingless reproductives is followed by DCF, or these prolong colony lifespan upon the death of independent founding winged queens.

(2) Loss of flight hints at dependent colony founding

Direct evidence for DCF is available for only a few of the species with wingless reproductives listed in Table 1. This dearth of field data can be attributed to the difficulty of observing an event that is both unpredictable in time and inconspicuous compared to the release of flying sexuals

(discussed in PEETERS & MOLET 2009). DCF has occasionally been documented in the field, e.g., *Cataglyphis floricola* (see AMOR & al. 2011), *Dolichoderus cuspidatus* (see MASCHWITZ & HÄNEL 1985), *Ocymyrmex picardi* (see BOLTON & MARSH 1989), *Proformica longiseta* (see FERNANDEZ-ESCUADERO & al. 2001). In other species, the occurrence of DCF is suggested by molecular data e.g., *Diacamma cyaneiventre* (see DOUMS & al. 2002), *Rhytidoponera mayri* (see TAY & al. 1997; see also Tab. 9.2 of PEETERS & MOLET 2009).

It is intuitive that ergatoid and brachypterous queens are incapable of claustral ICF: Without wing muscles, such metabolic reserves are not available to feed the first brood of workers. However, non-claustral ICF occurs in some species. Ergatoid foundresses of *Pogonomyrmex cunicularius* forage for seeds (JOHNSON 2010). Seeds are plentiful and seasonally predictable, meaning that the quantity of food collected outside by a foundress is likely to exceed any metabolic reserves. Non-claustral ICF by ergatoid queens was also reported in the predatory genera *Plectroctena* (in captivity; VILLET 1991) and *Myrmecia* (see HASKINS & HASKINS 1955): In these two genera, ergatoid queens are the same size as ancestral winged queens, and thus fully competent to hunt insects outside the nest. If unable to rely on the resorption of any wing muscles, an ergatoid foundress needs to forage outside the nest more frequently, thereby increasing her risks of mortality. We might expect that, in species where dispersal on foot away from the natal colony is insufficient to avoid local competition, DCF is selected instead (i.e., same dispersal distance, but better survival). Field data are required to determine whether the species capable of non-claustral ICF produce a large number of ergatoid gynes every year. In general, very few ergatoid gynes are reared annually in DCF species, in contrast to the large number of winged queens produced in ICF species (see below). A small investment in the ergatoid gynes of many species hints that they are not non-claustral founders.

To conclude, the lack of wing muscles in gamergates, ergatoid and brachypterous queens allows the intuitive prediction that they cannot do ICF in many species, but this needs to be verified with field observations. HEINZE & al. (2002) cautioned against deducing dispersal and founding tactics from queen morphology alone: In *Cardiocondyla batesii*, both brachypterous and winged queens disperse on the ground and seem capable of non-claustral ICF.

(3) Wingless reproductives can be cheaper per capita

In some genera ergatoid and brachypterous queens are the same size as the original winged queens, e.g., *Monomorium leae* (see FERSCH & al. 2000), *Myrmecia gigas* (= *brevinoda*) (see CLARK 1951), yet individuals are cheaper because they lack wing muscles. In *Cardiocondyla*, the thorax of brachypterous queens is reduced in size compared to conspecific winged queens (HEINZE & al. 2002, SEIFERT 2003).

In other genera, ergatoid queens are smaller than winged queens, e.g., *Acanthomyrmex* (see EGUCHI & al. 2008), *Monomorium viridum* (see DUBOIS 1986), *Myrmecina nipponica* (see MURAKAMI & al. 2002), *Pogonomyrmex pima* (see JOHNSON & al. 2007). Ergatoid queens even approximate worker size in *Ocymyrmex* and *Eutetramorium mocquersyi* (references in Tab. 1). In *Anochetus kempefi* and



Fig. 5: Ergatoid queen of *Simopelta* sp. nr. *pergandei* moving to a new nest accompanied by nestmate workers. © A. Wild.



Fig. 6: Ergatoid queen of *Labidus praedator* showing physogastry, i.e., the intersegmental membranes of gaster are exposed due to the highly developed ovaries. © S. Powell.

Mystrium oberthueri, ergatoid queens are smaller (except gaster in *A. kempfi*) than the workers. Since winged queens in closely related species are bigger than workers, these comparisons indicate that such ergatoid queens are reduced in size. In contrast, the ergatoid queens in dorylomorph and a few other genera can be huge compared to workers (Figs. 5 - 6).

In species with winged queens, DCF has been shown to be associated with a reduction in *per capita* energy investment (KELLER & PASSERA 1989). This reduction is much more pronounced in species with wingless reproductives. In species with ergatoid queens that are reduced in size, weight data are seldom available in the literature, e.g., fresh weights of 5.95 mg for *Mystrium* "red" ergatoid queens versus 14.51 mg for *M. rogeri* winged queens (MOLET & al. 2009). In *Cataglyphis floricola*, ergatoid gynes are six-fold lighter than the winged gynes of the closely related *C. emmae* (see AMOR & al. 2011). Generally, ergatoid gynes also have smaller post-emergence costs since they do not accumulate reserves prior to dispersal: glycogen stores for flying, fat and storage proteins for colony founding.

(4) Loss of wings is not linked to decreased fecundity

The reduced size of ergatoid and brachypterous queens is not accompanied by a reduction in fecundity. Many species have winged and wingless phenotypes with the same

number of ovarioles, e.g., *Myrmecina nipponica*, *Pogonomyrmex pima*. Ergatoid queens can be physogastric in some species, e.g., *Ocymyrmex*, *Onychomyrmex*, *Simopelta*, dorylomorphs (Fig. 6, KRONAUER 2009 Fig. 4, other references in Tab. 1), which is evidence of high fecundity. In various unrelated lineages, monogynous colonies can have tens of thousands of workers (e.g., some *Leptogenys*, *Dolichoderus cuspidatus*, most dorylomorph species). Comparing monogynous species, there is no evidence that wingless reproductives produce smaller colonies than congeners with winged queens. In *Technomyrmex brunneus*, ergatoid queens have low fecundity, but highly polygynous colonies reach a huge size.

From flying queens to wingless reproductives: strong decrease in mortality

Winged foundresses must survive two very different stages before they succeed to raise the first adult workers: (I) aerial dispersal, copulation with foreign males, search for a suitable nesting site; (II) after dealation, solitary life (claustral or non-claustral) spent feeding and protecting the brood. These two stages constitute distinct selective contexts. Moreover, metabolic reserves in the form of enlarged wing muscles cannot help during (I).

(1) High mortality of queens during aerial dispersal

Queens fly away from their natal nest both to increase their chance of mating with a non-relative, and to escape local competition during colony foundation. In the process they can colonize distant habitats, and newly mated ant queens are particularly good invaders relative to termites and other insects lacking long-term sperm storage, because they are freed from the constraint of meeting conspecific mates soon after they settle. Indeed, daughters of the initial foundress will be produced for many years, increasing the chance that some will encounter a conspecific male.

Any time spent outside the nest seems dangerous for queens and should be reduced to a minimum. There is great variability in the distance dispersed by queens before they dealate and begin a new colony. Hence the mating pattern of each species has a strong influence on female mortality. Male aggregations, widespread in formicoid clades, are the most efficient means to achieve completely random matings (panmixis) in a population. However, they are presumably associated with the highest rates of mortality, because longer flight increases the probability of predation, desiccation and other accidents. Moreover, the synchronized release of sexuals across colonies means that bird predators can become alerted. In species where larger numbers of gynes cannot be produced to compensate for high mortality, female calling may be selected for.

Queens that mate far away from their natal colony are highly unlikely to return to it (BOURKE & FRANKS 1995), hence DCF is not an option. PEETERS & MOLET (2009) discussed that female calling is the first step in the evolution of DCF. Several species are known (especially Formicinae and Myrmicinae) in which the queens have normal wings but do not fly, e.g., *Cardiocondyla batesii* (see HEINZE & al. 2002), *Formica paralugubris* (see CHAPUISAT & KELLER 1999), *Lasius neglectus* (see ESPADALER & REY 2001), *Plagiolepis pygmaea* (see THURIN & ARON 2009). In *Monomorium pharaonis*, queens mate and shed wings within their parental colony (BOLTON 1986). In *Dolichode-*

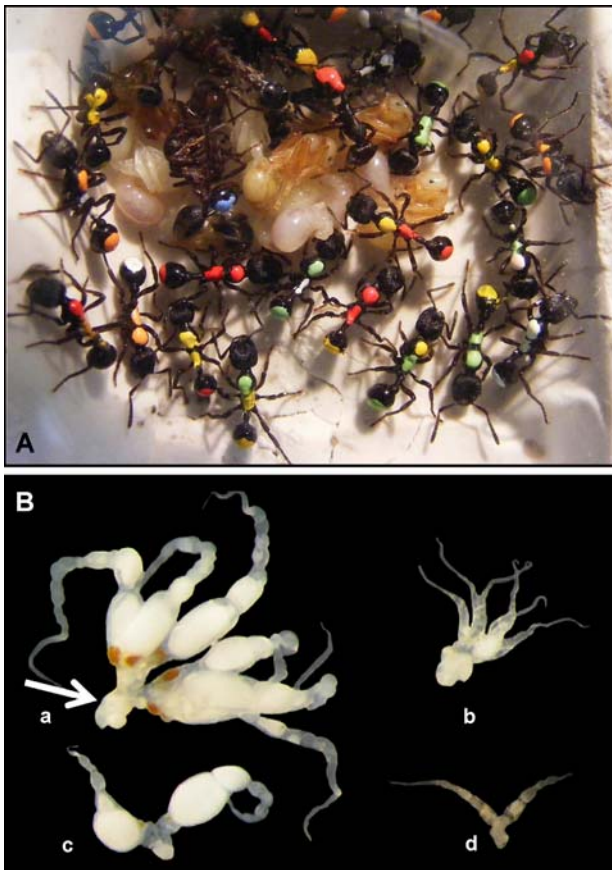


Fig. 7: (A) Ergatoid queens and workers are externally indistinguishable in *Eutetramorium mocquersyi*. (B) Dissections are needed to identify ergatoid queens (six ovarioles and a spermatheca; a & b) and workers (two ovarioles and no spermatheca; c & d). Arrow shows a spermatheca full of sperm. © A. Sébastien.

rus mariae, thousands of males were observed to fly away from their nests, but only very few gynes flew, and the majority stayed (LASKIS & TSCHINKEL 2008). Non-flying queens presumably mate inside or near natal nests (i.e., female calling) and DCF can follow. Unfortunately it is not known if these non-flying queens retain wing muscles. In *Formica truncorum*, the propensity of winged queens to disperse is influenced by their physiological condition: Smaller females with less fat and glycogen dealate more easily and mate without a preceding nuptial flight (SUNDSTRÖM 1995). The above examples indicate that shifts to DCF occur before the evolution of wingless reproductives. Moreover, many species that do DCF retain winged queens.

Unlike male aggregations, female calling could lead to some inbreeding if males do not fly far enough. Molecular evidence shows this not to be the case. In *Eciton burchellii*, the flying males alone can disperse genes and avoid inbreeding with ergatoid queens (BERGHOFF & al. 2008), and the same is found in *Cataglyphis cursor* (see CLÉMENCET & al. 2005) and *Diacamma cyaneiventre* (see DOUMS & al. 2002). Since males are winged in almost all ant species with wingless reproductives, they compensate for the very limited female dispersal. Hence the persistence of winged queens in most ants signify that they provide important benefits besides gene dispersal. Indeed they allow the colonization of disjunct or distant habitats.

(2) High mortality of queens during independent colony founding

Once mated and dealate, foundresses live as solitary insects as long as it takes for the first workers to emerge. As discussed earlier, formicoid species have queens that are highly adapted for claustral ICF. Moreover, the evolution of nanitic workers (i.e., smaller than normal) quickens the emergence of the first generation of workers. Various species evolved pleometrosis or parasitism to increase success rate of ICF (PEETERS & MOLET 2009).

In sharp contrast, queens are restricted to non-claustral ICF in poneroid and relatively few formicoid ants. Since foundresses raise offspring almost as large as themselves (caste dimorphism is limited in most poneroids), incipient colonies grow very slowly, and the solitary life of the queen lasts for several months (e.g., *Harpegnathos saltator*, see PEETERS & al. 2000). Field data are hard to obtain, but the success rate of non-claustral foundresses should be exceedingly low.

(3) Many winged queens are needed for independent colony founding

No matter how specialized claustral foundresses are, mortality is high during the dispersal flight. Existing estimates suggest that less than 0.1% of young queens succeed. Hence, a large number of winged gynes must be produced annually by each colony. Even species that have small colonies seem capable of a large reproductive investment, e.g., in *Harpegnathos saltator*, a few colonies of average size (65 ± 40 workers) produced more than 60 gynes (PEETERS & al. 2000).

(4) Few ergatoid queens are needed for dependent colony founding

Both female calling and DCF are likely to reduce queen mortality dramatically (predation risks during mating and independent founding are detailed earlier). Furthermore, producing many gynes makes no sense since only few of them (sometimes one) can disperse during division events. Empirical data are limited but indicate that colonies rear very few ergatoid gynes annually, e.g., army ants (KRONAUER 2009), *Aphaenogaster* (see CHÉRON & al. 2009), *Onychomyrmex* (see MIYATA & al. 2003), *Proceratium* (C. Peeters & B.L. Fisher, unpubl.). This reduced investment in female sexuals is further evidence for a decreased mortality rate.

An exception to this pattern is found in genera (especially in Myrmicinae) with ergatoid queens that are similar in size to conspecific workers (Fig. 7), e.g., *Eutetramorium*, *Mystrium*, *Ocymyrmex*. Many are produced annually but a substantial proportion do not mate, and they function as labourers. Since they do not disperse, these "multi-purpose" ergatoid queens can be as numerous as workers in the colonies; both virgin ergatoids and workers contribute to the success of DCF (MOLET & al. 2009). This contrasts with genera where "single-purpose" ergatoid queens are similar in size (or bigger) compared to ancestral winged queens, and are produced in very small numbers. There is no surplus of gynes, virgin ergatoids are rarely collected and colonies are generally monogynous (PEETERS & ITO 2001).

Wingless reproductives: with or without winged queens?

As seen in Table 1, winged queens exist as well as non-flying reproductives (i.e., AQ + EQ, AQ + BQ [short-

winged queens] or AQ + G) in more species (belonging to 26 genera) than commonly thought. In other species, winged queens have been completely replaced by wingless reproductives. Many authors (e.g., HEINZE 1993) discussed dispersal polymorphism, which is widespread in ants. However, the permanent loss of winged queens in other ants is less considered.

(1) Dispersal polymorphism

Flying and non-flying morphs alternate during the life history of many solitary insects. The lack of development (or the resorption) of wings and flight muscles amounts to a trade-off for higher reproductive success, for example, more active ovaries (ROFF 1986). In *Drosophila melanogaster*, both flight and egg production depend on the same energy reserves, hence dispersal reduces fecundity. There is no such linkage in DCF ants because fecundity is a function of the resources gathered by infertile helpers: Flightless reproductives in many species have the same number of ovarioles as winged queens. Their evolution is a colony-level adaptation, redirecting resources towards the production of more workers to ensure the success of colony division. MOLET & al. (2008) discussed how species adapt to decreasing success in ICF. They can alter the quantity or quality (size or fat reserves) of gynes, or shift to DCF provided gynes mate near their natal nests.

Many ants have winged queens that are polymorphic, often to combine the benefits of ICF and DCF (HEINZE & KELLER 2000). Intraspecific queen polymorphism ranges from differences in wing muscle development (e.g., *Formica truncorum*; see JOHNSON & al. 2005), to bimodal distributions of size (macro- and microgynes, both of which can fly; RÜPPELL & HEINZE 1999). Interspecific comparisons indicate that DCF is associated with winged queens that have modified physiology (fat and carbohydrate stores, KELLER & PASSERA 1989, PASSERA & KELLER 1990) or thorax volume (STILLE 1996). An adaptation more extreme than any physiological or morphological modifications of winged queens is a dimorphism winged / wingless reproductives. Less dramatic is the coexistence of winged queens and gamergates (MONNIN & PEETERS 2008), but this is an option only for the relatively few species in which workers have a functional spermatheca.

A winged / wingless polymorphism in reproductives evolved independently across lineages, corresponding to a variety of selective contexts. Ergatoid queens, brachypterous queens and gamergates are usually cheaper than winged queens, and can function as secondary reproductives in various species, to extend colony lifespan after the death of the winged foundress (i.e., inheritance of colony resource). These secondary reproductives do not engage in ICF. In *Technomyrmex brunneus*, colonies with millions of adults are started by single dealate foundresses that exhibit small size dimorphism relative to workers; they are short-lived and soon replaced by large numbers of ergatoid queens, produced throughout the year, variable in size and mated with brothers (TSUJI & al. 1991, YAMAUCHI & al. 1991). In *Harpegnathos saltator*, several gamergates inbreed and replace the dealate foundress (PEETERS & al. 2000). Similarly in many lower termites, wingless neotronics of both sexes inbreed and function as secondary reproductives (KORB & HARTFELDER 2008). Nonetheless, in most ants secondary reproductives are reported to outbreed.

Dispersal polymorphism can take other forms. In several genera, winged or wingless reproductives occur over gradients of altitude or latitude, presumably because ICF or DCF provide different adaptive benefits in different habitats. In *Myrmecina nipponica*, ergatoid queens only exist in areas of low temperature or high altitude (MURAKAMI & al. 2002), but in *M. graminicola* they occur in the same habitats as winged queens (BUSCHINGER & SCHREIBER 2002). In *Monomorium emersoni*, ergatoid queens are found at higher altitude (S. Cover, pers. comm.). In contrast, in *M. sp. 10* (= *leae*), monogynous colonies with winged queens and polygynous colonies with ergatoid queens coexist in the same habitats in the Australian Alps (FERSCH & al. 2000). In *Megalomyrmex goeldii*, either winged or ergatoid queens occur in different parts of the range (BRANDÃO 1990). In *Myrmica kotokui*, winged queens differed in wing size between populations; shorter-winged queens mated near their natal nest, leading to secondary polygyny (KIKUCHI & al. 1999). In *Harpagoxenus sublaevis* and *Leptothorax* sp. A, winged queens are more frequent in some populations than others. Seasonal fluctuations affect colony structure: While some queens disperse and attempt ICF immediately after mating, others are adopted into established nests (HEINZE & BUSCHINGER 1987). In the genus *Rhytidoponera*, most species reproduce exclusively with gamergates and DCF, but in the basal *R. impressa*-group, either winged queens (ICF) or gamergates (DCF) reproduce (separate colonies). The proportion of queen colonies decreases from tropical north to temperate south, indicating a decrease in ICF success (MOLET & al. 2008).

In other species where winged queens occur together with wingless reproductives, it is not always known if they are produced regularly, or in large numbers. In many species, the occurrence of two reproductive morphs is based on museum specimens, and it is unknown whether they reproduce in the same colonies, or in separate populations. Many additional data are needed before we can study variations in the proportion of wingless reproductives across different habitats.

Wingless reproductives evolved convergently, hence the links with ecological parameters and life history are multiple and varied. There is little consensus in the literature about what environmental factors favour either ICF or DCF. The association between ICF/DCF and habitats that are patchy or unstable is inconsistent (see MOLET & al. 2008). DCF allows for better local propagation, but selection favours the retention of a low rate of aerial dispersal (HEINZE & TSUJI 1995). ICF allows for maximum dispersal of the queens, before and immediately after copulation. In addition to mortality patterns, the spatio-temporal distribution of suitable habitats affects the relative success of ICF / DCF (NAKAMARU & al. 2007).

(2) Evolutionary loss of winged queens

Unlike the dispersal polymorphism discussed by HEINZE & KELLER (2000), there are species where winged queens disappear completely. These have been permanently replaced by wingless reproductives with the same phenotypes as those that coexist with winged queens in closely related species. This parallels the situation in solitary insects: If a habitat is stable for long periods or distributed so that an individual can move from one patch to another by walking, hopping or swimming, a flight polymorphism can

shift towards the wingless or brachypterous morph (ROFF 1986). An extreme result of this shift may be the complete loss of the flying morph and an entirely wingless population or species.

In ants, the permanent loss of winged queens is strong evidence of an evolutionary shift from ICF + DCF to obligate DCF. Total reliance on brachypterous queens, ergatoid queens, or gamergates, is an extreme adaptation for DCF because it becomes obligate (exceptions were discussed earlier). The loss of winged queens is apparently irreversible and eliminates the option of colonizing disjunct habitats. This probably explains why many ant species exhibit a mixed strategy (ICF + DCF) by retaining winged queens. Both semi-claustral and claustral ICF have been completely replaced by DCF, meaning that winged queens can be selected against irrespective of their degree of founding specialization.

Species having only wingless reproductives are exceptional in some genera (e.g., *Myrmica*, *Odontomachus*, *Polyrhachis*, *Tapinoma*, *Tetraponera*) but predominate in others (e.g., *Cerapachys*, *Leptogenys*, *Leptomymex*, *Tertaner*). All dorylomorph genera lack winged queens (Tab. 1), suggesting that ergatoid queens replaced winged queens in basal species. Besides dorylomorphs, only eight genera lack winged queens entirely, e.g., *Dinoponera*, *Simopelta*, *Ocymymex* (Tab. 1). In *Leptogenys* (205 species), less than a handful of species have winged queens and all others have either ergatoid queens or gamergates. All 15 species in the *Dolichoderus cuspidatus*-group have ergatoid queens, linked to obligate DCF because of nomadism and symbiotic mealybugs (MASCHWITZ & HÄNEL 1985); among the remaining 100 species of this genus, only *D. doriae* is known to have ergatoid queens (CLARK 1934). It appears that species without winged queens are often scattered in clades that mostly retain them. There may be a high probability that loss of winged queens will lead to extinction over evolutionary time. Ergatoid queens only become widespread in a genus if associated with a specific life history, e.g., nomadism (absence of valuable nests) or mass predation.

Current evidence reveals that species exhibiting obligate DCF inhabit a great diversity of habitats, not just deserts, islands and high mountains. There are no conclusive data about a disproportionate number of species with wingless reproductives distributed in harsh arid environments. Future research should compare the ecological profiles of congeneric species having winged / wingless reproductives, or wingless reproductives only; comparing less related clades is often meaningless.

(3) Parasitism is no explanation for queen polymorphism

The evolution of wingless reproductive phenotypes has sometimes been assimilated with intraspecific parasitism, and not interpreted as an adaptation for DCF. Much emphasis was put on the idea that species with macro- and microgynes (i.e., queen polymorphism) are precursors for the evolution of host-parasite species pairs (e.g., HEINZE & KELLER 2000). While this may be the case in genera such as *Leptothorax* and *Myrmica*, evidence in Table 1 suggests that species having both winged and wingless reproductives are usually ancestral to free-living species in which DCF is obligate. BOLTON (1986) discussed that ergatoid queens in the *Monomorium salomonis*-group had been au-

tomatically treated as social parasites and described as new species or new genera; instead, he correctly identified a shift in dispersal strategy, with recently mated queens returning to the parental colony after female calling. Flying ability seems valuable for parasites since it helps them to locate alien colonies, and it is not intuitive that they should lose winged queens. Indeed, two species in *Monomorium salomonis*-group are confirmed workerless inquilines, and their queens are winged (BOLTON 1986).

Conclusions and outlook

Aerial dispersal and ICF bring many benefits, e.g., colonize new habitats, but it is becoming clear that this was selected against in a lot of ant species. Good evidence is the existence of wingless reproductives in many lineages, but there are probably plenty more undiscovered cases of winged queens mating on the ground, followed by DCF. Females take fewer risks by mating close to or inside the natal nests. Flying queens are not essential in ants because flying males disperse sufficiently to prevent inbreeding. In species where ICF (together with a considerable investment in gynes) was selected against, DCF evolves, either facultative or obligate depending on species.

This literature review indicates that (1) ergatoid queens (or short-winged morphs unable to fly) and gamergates reproduce together with winged queens in a large number of unrelated lineages of ants; (2) these same wingless reproductives have completely replaced winged queens in an equally large number of taxa. The two phenomena are clearly connected, as shown by congeneric species exhibiting one or the other.

My explanation for the recurrent evolution of wingless reproductives centers on the shift to DCF. In all ants, DCF implies that reproductives disperse on foot together with nestmate workers, hence the production of expensive winged queens that are well-equipped for ICF stops being adaptive. Ergatoid and brachypterous queens uncouple the morphological traits underlying flight and reproduction. In many species they are cheaper *per capita* than the winged queens they supersede (no wing muscles, and frequent reduction in total size), with only little or no reduction in fecundity. Importantly, wingless reproductives cannot start colonies without nestmate workers, and their evolution is tantamount to a new strategy of reproductive investment.

The following empirical investigations are suggested:

(1) Flight reduction probably occurs in many more species of ants. Studying inter-individual differences in wing muscle development may yield good insights on dispersal polymorphism.

(2) Although field data are needed about colony foundation in more genera, added emphasis should be given to the external morphology of reproductives because this gives clear evidence about behavioural strategies. The general expectation is that wingless reproductives do DCF and cannot survive without nestmate workers. However, a few species are non-claustral founders. This variability in the loss of autonomy of reproductives must be investigated across species, keeping in mind the distinction between "single-purpose" and "multi-purpose" ergatoid queens (MOLET & al. 2009). Comparisons with honeybees and stingless bees are heuristic, because their winged queens are highly specialized for DCF and cannot survive without nestmate workers.

(3) Species with conspecific morphs are particularly suitable to compare patterns of reproductive investments. Sexual investment in related species with and without winged queens requires data on both the costs *per capita* of reproductives, and the numbers produced annually. Nonetheless, estimating the cost of additional workers is always problematic because they are involved in both maintenance and reproduction.

(4) Incomplete knowledge of the distribution of wingless reproductives across taxa precludes an estimate of the minimum number of independent evolutions. Are wingless reproductives more common in formicoid or poneroid sub-families? Is all the variation at the tips?, or are there some deeper evolutionary trends as in dorylomorphs?

(5) As detailed phylogenies of genera become available, better evolutionary scenarios can be investigated. Currently there is no evidence of a progression from microgynes to brachypterous queens to ergatoid queens. These different morphs evolved independently in lineages having winged queens.

It is revealing that the most speciose ant genera (*Pheidole*, *Camponotus* and *Crematogaster*) are not known to have any species with flightless queens. Why? They all have in common a large degree of dimorphism between winged queens and workers, together with claustral ICF. DCF is currently unreported, although evidence is probably incomplete. How can these taxa succeed better in claustral ICF? Can they simply produce enough sexuals to compensate for high mortality?

The shift to obligate DCF can be an evolutionary dead end, but its occurrence in many ants indicates that novel reproductive phenotypes relying heavily on the worker caste can be advantageous. All social Hymenoptera that shift to DCF exhibit colony-level adaptations, i.e., different proportions of workers and gynes are produced. Only the ants show striking individual-level adaptations in addition, i.e., novel reproductive phenotypes that cannot fly, together with the sporadic loss of winged queens.

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