

# DO PERMANENTLY MIXED COLONIES OF WOOD ANTS (HYMENOPTERA: FORMICIDAE) REALLY EXIST?

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**Abstract.**— We describe the composition of two colonies of wood ants (FM-1 and FM-2) from southern Finland, identified on the basis of morphological investigations of workers (for FM-1, also of alate gynes and males) as mixed colonies comprising individuals with phenotypes typical of *Formica aquilonia* Yarr., *F. polyctena* Först. and *F. rufa* L. The prevailing species (phenotypes) were *F. polyctena* in FM-1, and *F. rufa* in FM-2. Colony FM-1 was observed every year in the period 1996–2006, almost from the moment it was formed. A first tentative investigation in 1999 revealed that it was already a mixed one and was probably also polygynous. Systematic follow-up investigations from 2002 to 2006 demonstrated relative stability of the proportions of individual species (phenotypes). A possible origin of this permanently mixed colony is postulated and discussed.



**Key words.**— Ants, Formicidae, *Formica rufa*-group, *Formica polyctena*, *Formica aquilonia*, *Formica rufa*, mixed colonies, polygyny, morphology, phenotypes.

## INTRODUCTION

Palaeartic wood ants, i.e. the species of the subgenus *Formica* s. str., and especially the members of the *Formica rufa*-group (sensu Dlussky 1967), have been the object of intensive studies since the very early days of myrmecology and have been discussed and described in numerous papers. Even so, they still pose a taxonomic problem, and often puzzle field researchers. Vepsäläinen and Pisarski (1981) called the *F. rufa* group “a taxonomic enfant terrible” among wood ants and likened the state of taxonomy of these species to “chaos before order.”

Diagnosis of the *F. rufa*-group is based on the hairiness and, to a lesser degree, on the microsculpture of various parts of the body, mainly in workers (e.g. Yarow 1955, Dlussky 1967, Dlussky and Pisarski 1971, Kutter 1977, Collingwood 1979, Douwes 1981, Seifert 1996, Czechowski *et al.* 2002, Radchenko *et al.* 2004). However, the generally high morphological similarity among species within the group together with consider-

able intraspecific variability of individuals often make it difficult, and sometimes impossible, to determine the species affiliation of a given colony. Such difficulties are especially spectacular in certain geographic regions, where they usually concern particular pairs (or triplets) of species, e.g. *F. rufa* L. and *F. polyctena* Först. in Central Europe and southern Sweden, *F. aquilonia* Yarr., *F. lugubris* Zett. and *F. paralugubris* Seifert in the Alps, *F. polyctena* and *F. aquilonia* in Finland (Gösswald *et al.* 1965, Rosengren 1977, Douwes 1979, Pamilo *et al.* 1979, 1992, Vepsäläinen and Pisarski 1981, Maeder *et al.* 2005). It occurs that workers from the same nest bear intermediate species characters or that individuals within a colony seem to represent different species. Moreover, it happens that the appearance of workers within a colony changes in time, and nest samples from different years may be differently identified (Pamilo and Vepsäläinen 1977, Vepsäläinen and Pisarski 1981, Czechowski 1996).

Recent investigations, both morphological and molecular, have thrown some light on this problem. On

the one hand temporary social parasitism, i.e. taking over colonies (queenless or queenright ones) by heterospecific gynes (see Pisarski and Czechowski 1994, Czechowski 1993a, b, 1996), has been shown to occur within the subgenus *Formica* s. str., one result being the establishment of temporarily mixed colonies. On the other hand the possibility of interspecific hybridization within the *F. rufa*-group has been evidenced (e.g. Seifert 1991, 1999, Czechowski 1993c, 1996, Goropashnaya *et al.* 2004, Gyllenstrand *et al.* 2004, Seifert and Goropashnaya 2004, Sorvari 2006). Nevertheless, not all cases encountered in the field can be conveniently explained in terms of one of the above phenomena. Frequent polygyny in wood ant colonies, which is partly due to geographical factors (e.g. Pisarski 1981, Mabelis 1986, Mabelis and Soesbergen 1989, Pamilo *et al.* 1992, Rosengren *et al.* 1993; see also Czechowski 1996), and multiple mating (polyandry) of wood ant gynes (Yamauchi *et al.* 1994, Boomsma and Sundström 1998) further compound the problem.

Anyway, colonies are found here and there which evidently appear to be (at least potentially) permanently comprised of different species. The present paper offers circumstantial proof of the existence of such mixed wood ant societies, drawing this conclusion from long-term observations of the morphological composition of a particular colony.

## STUDY AREA, MATERIAL AND METHODS

The study was conducted in the vicinity of Tvärminne in the region of Hanko Peninsula in southern Finland, where annual Polish-Finnish myrmecological investigations have been carried out since the late 1970's. This region is well-known to Finnish and visiting foreign myrmecologists (K. Vepsäläinen, P. Pamilo, W. Fortelius, J. Sorvari, C. Collingwood, E. O. Wilson, B. Pisarski, W. Czechowski, and others) for unusually frequent and often inexplicable inter- and intracolony variability of the local wood ants of the *F. rufa* group, represented there by *F. rufa*, *F. polyctena*, *F. aquilonia* and *F. lugubris* (see Czechowski 1996).

The main object of the present study was colony FM-1 on the island of Vikaskär, a 2-hectare rocky island within the Tvärminne archipelago, two-third forested, situated 50 m off the mainland (Långholmen peninsula) and 60 m from the big (10 ha) island of Joskär, both densely populated by wood ants. The mainland supports all Finnish species of the *F. rufa*-group. Joskär, at the time of the present investigations, was populated by a polydomous *F. polyctena* colony; earlier, in the seventies and eighties, there were also single nests of *F. lugubris* and *F. aquilonia* (Pisarski and Vepsäläinen 1989 and unpubl. data). The island of Vikaskär itself had two monodomous colonies of

*F. polyctena*, artificially established in 1987 (see Czechowski 1990); at the time of colonization, the ants were identified as *F. aquilonia*, and they spontaneously transformed into morphologically typical *F. polyctena* within the period of study. There had also been one natural *F. lugubris* colony on the island before, but it died out in the early nineties. The two existing colonies of *F. polyctena* produced their own numerous reproductives (both gynes and males).

Colony FM-1 was noticed for the first time as an almost incipient colony (however, already with no *Formica fusca* L. workers) in 1996. It was situated between the territories of the two already existing *F. polyctena* colonies, outside the searching range of both. In 1999, the colony moved from a forest onto a sparsely overgrown open rocky outcrop, and later its size began to increase dramatically. In the meantime, colony FM-1 had moved 2–3 times before finally (in 2000) settling in the former nest site of *F. lugubris*, while still remaining monodomous. In 2004, its mound had reached ca. 1 m in diameter and 45 cm in height (compared to 40 and 20 cm, respectively, in 2000) and maintained these dimensions until 2006 (Fig. 1). The territory of FM-1 enlarged considerably, pushing aside the territories of both *F. polyctena* colonies.

J. Sorvari (personal comm.) was the first to notice, in 1999, that FM-1 consisted of workers that seemed to represent different species. Then the mixed nature of the colony was confirmed when nest samples taken in the years 2002, 2004, 2005 and 2006 were morphologically analysed. In the years 2002–2005 the samples were collected in July, when only workers were available. The nest sample of 2006 was taken in mid-June, and it included workers as well as alate sexuals, gynes and males, which were having their nuptial flights at that time.

Another 'mixed' colony, FM-2, is also considered in this paper. It was situated on the mainland within a complex of sand dunes being overgrown with pine forest close to Tvärminne village. There were several typical mono- or oligodomous *F. rufa* colonies in the immediate vicinity (see Czechowski and Markó 2005). *F. polyctena* also occurred there, with its nearest colonies at a distance of ca. 250 m. FM-2 was followed up at that location from 2002 to 2004. In 2005, the colony disappeared, leaving an intact nest. The colony was not too big (mound diameter ca. 50 cm, height 25 cm; Fig. 2), but very active, so most probably it moved somewhere else. A worker nest sample of FM-2 was taken once in 2004.

Nest samples (including worker samples containing at least 100 individuals per sample; Table 1) were taken from the mound surface. Individuals were subsequently classified into morphological groups corresponding to different species based on commonly accepted key criteria, especially the presence, numbers



Figure 1. Nest of colony FM-1 in 2004 (photo W. Czechowski).



Figure 2. Nest of colony FM-2 in 2004 (photo W. Czechowski).

and appearance of standing hairs on the occipital margin of the head, the ventral surface of the head and the pilosity of the dorsal part of the alitrunk (see e.g. Dlussky 1967, Dlussky and Pisarski 1971, Collingwood 1979, Seifert 1996, Czechowski *et al.* 2002).

As regards fertilized queens of colonies FM-1 and FM-2, they were unavailable for different reasons: the former nested on a rocky ground with the underground part of its nest in rocky crevices, and the latter was the object of an ecological study going on at the same time (colony FR-2 in Czechowski and Markó 2005) and no interference was possible.

## RESULTS

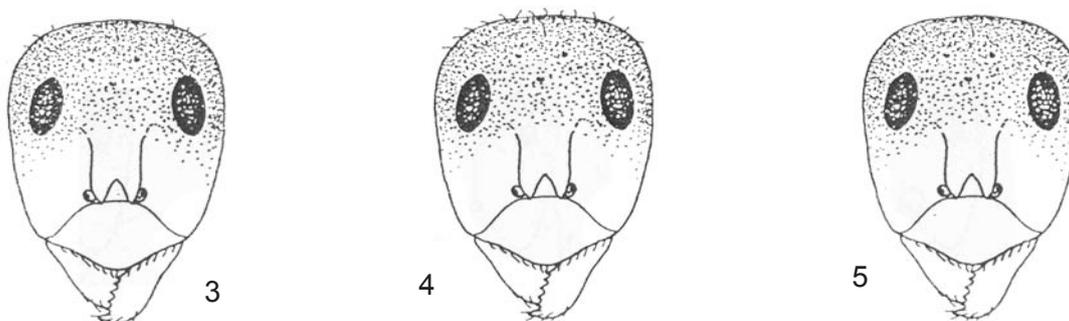
Within both colonies (FM-1 and FM-2) two main morphological groups of workers were explicitly distinguishable, albeit in different proportions. One of those groups was homogenous and embraced individuals with short erect hairs on the occipital head margin (from at least a few hairs on the occipital corners to abundant hairs along the whole margin) and the alitrunk dorsum covered entirely with fairly abundant hairs – i.e. morphs corresponding completely to the phenotype of *Formica aquilonia* (Figs 3, 4, 6, 7). The

second group was considerably differentiated, and this differentiation represented a continuous (with no hiatus) transition from the typical phenotype of *F. polyctena* to that typical of *F. rufa*. This latter group was arbitrarily divided into two categories: following the classical taxonomic approach, individuals with a completely hairless occipital head margin, a hairless or almost hairless ventral surface of the head (with at most short sparse suberect hairs) and a hairless or almost hairless alitrunk (with no more than a few standing hairs on the pronotum or mesonotum) were classified as *F. polyctena* (Figs 5, 8, 9), and those with a completely hairless occipital head margin, a ventral surface of the head with quite long erect hairs and not less than ten standing hairs on the pronotum and mesonotum respectively were regarded as *F. rufa* (Figs 5, 10, 11).

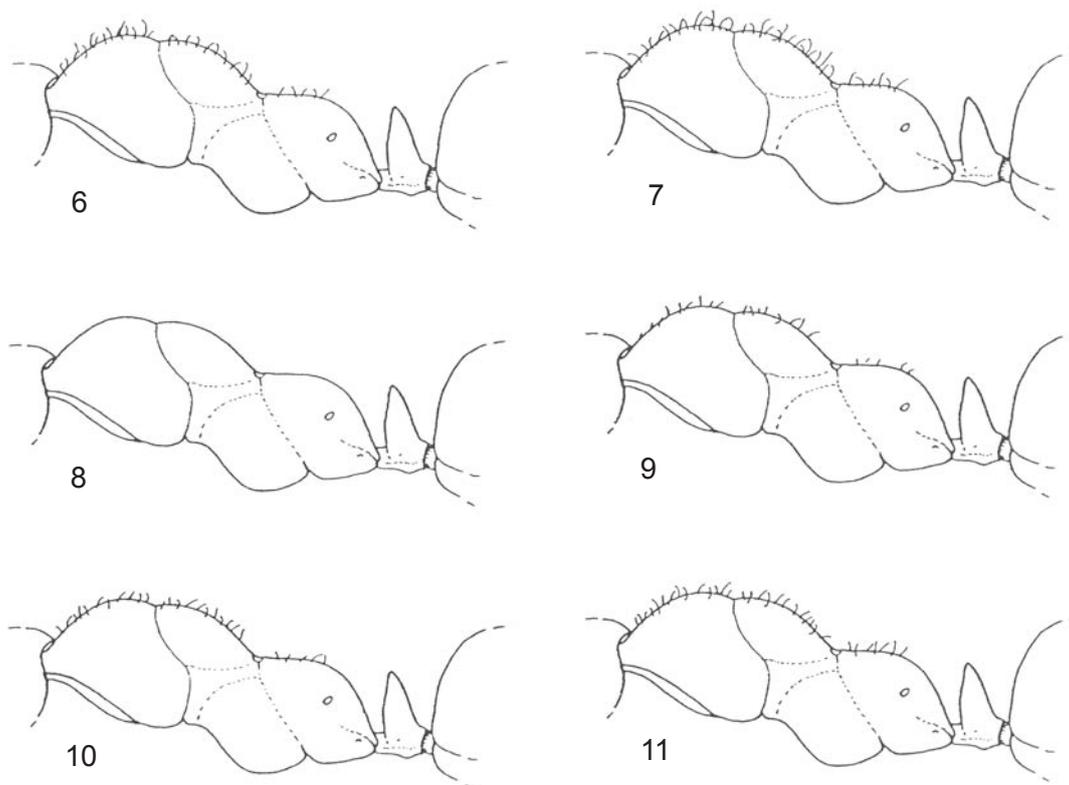
Workers of the *F. polyctena* type clearly prevailed in FM-1, whereas those of the *F. rufa* type prevailed in FM-2. It should be emphasized, however, that colony FM-1 maintained its mixed character over several years, and the proportions of the particular worker morphs, despite some fluctuations, remained at a relatively steady level (Table 1), their average proportions being as follows: *F. polyctena* – 75%, *F. aquilonia* – 22.5%, *F. rufa* – 2.5%.

Table 1. Proportions (in round figures) of different species (phenotypes) among workers in the colonies studied (numbers of individuals in the parentheses) in particular years.

Colony, year Species (phenotype)	FM-1					FM-2
	2002	2003	2004	2005	2006	2004
<i>F. aquilonia</i>	21% (21)		31% (35)	14% (20)	24% (62)	4% (5)
<i>F. polyctena</i>	78% (78)	no data	65% (74)	84% (117)	73% (188)	38% (45)
<i>F. rufa</i>	1% (1)		4% (5)	2% (3)	3% (7)	58% (68)
Sample size (n)	100	–	114	140	257	118



Figures 3–5. Hairiness of head occipital margin of workers from colonies FM-1 and FM-2. (3–4) Phenotype of *F. aquilonia* (range of variability); (5) phenotype of *F. polyctena* or *F. rufa*. See also Figs 6–11.

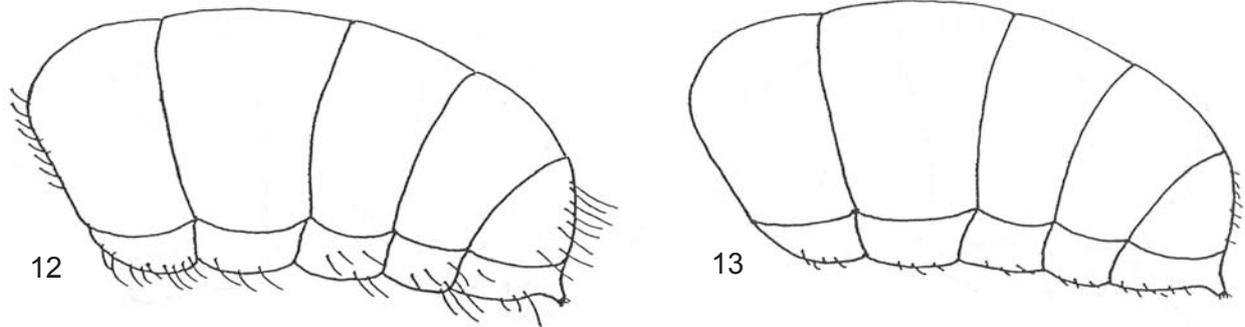


Figures 6–11. Hairiness of alitrunk dorsum of workers from colonies FM-1 and FM-2. (6–7) Range of variability within the phenotype of *F. aquilonia*; (8–9) Range of variability within the phenotype of *F. polyctena*; (10–11) Range of variability within the phenotype of *F. rufa*. See also Figs 3–5.

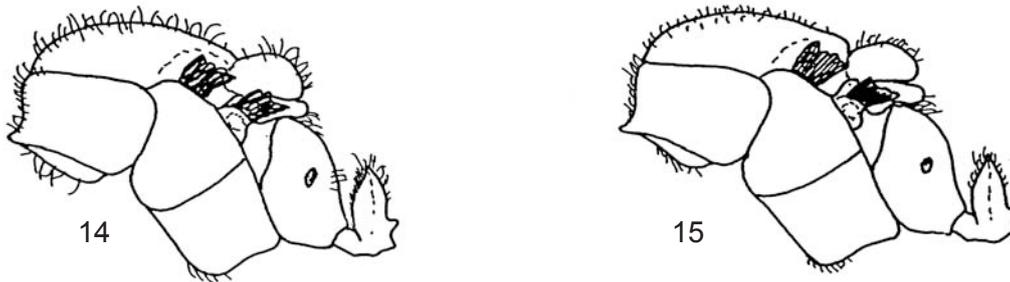
The same two main morphological groups seen in workers were distinguished within the alate sexuals, both gynes and males, sampled from FM-1. Among the gynes, some individuals bore typical features of *F. aquilonia*, most notably the declivity of the first gastral tergite with short standing hairs and relatively long hairs on all gastral sternites and the last tergite (Fig. 12). The others had no standing hairs on the first gastral tergite declivity, and much shorter hairs on the gastral sternites and the last tergite, which corresponded to *F. polyctena* or *F. rufa* (Fig. 13). As for the males, there were individuals with much longer

standing hairs on the dorsal part of the scutum that were classified as *F. aquilonia* (Fig. 14), and ones with much shorter hairs there, classified as *F. polyctena* or *F. rufa* (Fig. 15). As the sexuals of *F. polyctena* and *F. rufa* are hardly distinguishable, both gynes and males in this group were grouped together (*F. polyctena/rufa*) (Table 2).

It is worth stressing that, in FM-1, the proportions of the particular morphs within each of the female castes, i.e. workers and alate gynes, were identical: *F. polyctena/rufa* – 76%, *F. aquilonia* – 24% (in 2006). The proportion of males (nearly twice less



Figures 12–13. Hairiness of gaster of gynes from colony FM-1. (12) Phenotype of *F. aquilonia*; (13) phenotype of *F. polyctena* or *F. rufa*.



Figures 14–15. Hairiness of alitrunk of males from colony FM-1. (14) Phenotype of *F. aquilonia*; (15) phenotype of *F. polyctena* or *F. rufa*.

abundant than gynes at the time of sampling) was somewhat different, 56.5% and 43.5% respectively (Table 2). However, this difference was statistically insignificant ( $\chi^2 = 2,65, P > 0.1$ ).

## DISCUSSION

If individuals of an *F. aquilonia* phenotype of colonies FM-1 or FM-2 formed a separate colony, they would doubtless be identified as a colony of *F. aquilonia*. Similar autonomous colonies of inhabitants of FM-1 or FM-2 with phenotypes more or less resembling *F. polyctena* and *F. rufa* would be determined to be colonies of *F. polyctena* or *F. rufa*, respectively. Determining the species affiliation of a colony formed by individuals of an intermediate phenotype between those of *F. polyctena* and *F. rufa* would be problematic, but such “problem colonies” which look like something between one species and the other, are by no means a rarity in the study area (see Introduction),

and are found not only in wood ants. Such problematic colonies of wood ants, transitional between *F. polyctena* and *F. rufa*, can be interpreted as colonies of hybrids, hybridization among the *F. rufa* group being a known fact (see Introduction). Accordingly, some ‘intermediate’ individuals of colonies FM-1 and FM-2 arbitrarily assigned to *F. polyctena* or *F. rufa* might as well be regarded as hybrids of *F. polyctena* × *F. rufa*. [It has to be pointed out, though, that species distinctness of these two taxa has been questioned (e.g. Seifert 1991; see also Czechowski 1996)].

Thus, there are no **morphological** grounds for not treating the two colonies as mixed-species colonies. There is not much to be said regarding colony FM-2. As regards FM-1, it seemed to be a permanently (for 8 years, most probably even longer) mixed polygynous colony containing fertilized queens of *F. aquilonia*, *F. polyctena* and *F. rufa* (or perhaps hybrids of the two latter) coexisting in the same nest. It was a fully functional colony, producing its offspring of both castes, workers and reproductives, and, in the case of the

Table 2. Proportions of different species (phenotypes) within particular sexes and castes in colony FM-1 (data from 2006).

Sex, caste Species (phenotype)	Females		Males
	Workers	Gynes	
<i>F. aquilonia</i>	24.1% (62)	23.8% (10)	43.5% (10)
<i>F. polyctena/rufa</i>	75.9% (195)	76.2% (32)	56.5% (13)
Sample size (n)	257	42	23

latter, of both sexes. The proportions of individual species (phenotypes) among young sexuals corresponded to those among workers.

This peculiar mixed-colony status could be primary or secondary. The former possibility would mean that the supposed heterospecific fundatrices had already grouped together while taking over a colony of *F. fusca*. Young gynes of wood ants are sometimes reported trying to get inside nests of their host species in large numbers (Pisarski and Czechowski 1994). The latter possibility suggests a scenario where various gynes were adopted by an existing monospecific wood ant colony, especially if that colony had lost its own queen(s). The adoptive capacity of queenright, even polygynous, wood ant colonies is normally limited, including a time limit (the period of 'opening up') (Fortelius *et al.* 1990, 1993, Cherix *et al.* 1991). The 'opening up' of queenless colonies is wider as orphanhood annuls the natural mechanisms of selection and enhances the workers' tolerance to new gynes. Such colonies may even adopt gynes of related species (Czechowski 1993a, b, 1996).

At any rate, the finding of an explosive growth of colony size strongly suggests that FM-1 enlarged its pool of fertilized queens at some time. The queens must have come from outside of the colony as it is very unlikely that the colony, which was probably 3 years old at the time, was able to produce its own gynes. The most likely hypothesis is that the adopted gynes (with some more adopted over time) came from two nearby colonies of wood ants – first of *F. aquilonia*, and then of *F. polyctena*. It may be no coincidence that each of the two 'mixed' colonies was dominated by the species whose nests were found close to it: *F. polyctena* in the case of colony FM-1 and *F. rufa* in the case of colony FM-2.

Genetic analyses of individuals representing different phenotypes within the two under discussion colonies are going to be carried out. The results might be especially interesting in the context of recently revealed possible phenotype/haplotype mismatches in wood ants (see Seifert and Goropashnaya 2004).

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