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Frequent occurrence of gynandromorphs in the natural population of the ant *Vollenhovia emeryi* (Hymenoptera: Formicidae)

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Summary

Many gynandromorphs were obtained from the natural population of *Vollenhovia emeryi* (*microgyna* form) in Gifu, Japan. They were primarily male: most had the thorax and gaster of males, and the head contained tissues partially feminized to varying degrees. These gynandromorphs were found in 27 of 45 colonies studied (60.0%). Their proportion to total males in each colony varied from 3.7–47.7%, with a mean of 21.4% ($n = 21$). The gynandromorphs were found in all study areas and in every study year, suggesting that gynandromorphism in this species is not a rare phenomenon. Moreover, this observation suggests that gynandromorphs may occur more frequently in micraners than in macraners.

Introduction

Gynandromorphs have been reported from 42 ant species in 22 genera (Jones and Phillips, 1985). There are many papers about gynandromorphism in ants but normally related to one or a few individuals among many species. The frequency of their occurrence in the natural population seems to be very low. In Japan, gynandromorphs have been recorded from *Vollenhovia emeryi* (Kubota, 1984), but the details remain unclear.

Through our recent study on *V. emeryi*, we found extraordinarily frequent occurrences of gynandromorphs among the natural population. Here, we describe various types of gynandromorphs and their frequency and provide a brief discussion of certain aspects of the gynandromorphism in this species.

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Materials and methods

Vollenhovia emeryi is widespread in Honshu, Japan. Intraspecific morphological and social variations are large (The Myrmecological Society of Japan, 1992). According to Kinomura et al. (pers. comm.), two forms of the queen caste exist, macrogynes with normal wings and microgynes with aberrant short wings (see also Kubota, 1984; Kinomura and Yamauchi, 1992). The former typically forms monogynous colonies in mostly mountainous forests, whereas the latte is polygynous and colonizes mostly riverside forests and the margins. General relationships between them are similar to those in *Myrmica rubra* (Brian and Brian, 1955). Herafter, we call the form with macrogynes and the form with microgynes *macrogyna* and *microgyna*, respectively, following Brian and Brian (1955). However, these two forms may be classified into two separate species in future studies.

Moreover, *microgyna* colonies have size-dimorphic, winged males (macraners and micraners), whereas *macrogyna* colonies have only macraners. The wings of all males were normally long. The mean head width was 0.53 mm in macraners and 0.45 mm in micraners. The boundary is at 0.50 mm. Each colony produced mostly one of these types. Whenever a colony produced both types, one type occupied the greater portion. Therefore, we distinguished macraner and micraner colonies based on difference in the head width of males, but excluding gynandromorphs.

Winged sexuals of *V. emeryi* are produced from late August to late September and they remain in the colony until the following spring. We collected all colony members of the *microgyna* form from nests in three riverside forest areas (Gifu, Kaizu and Kagamihara) along the Nagara and the Kiso Rivers, as well as members of the *macrogyna* from several mountainous forests in Gifu, central Japan, during winters from 1990 through 1993. All adult members were examined using a dissecting microscope and a scanning electron microscope, and the morphology of each gynandromorph was recorded.

Results

We collected 35 and 89 *microgyna* colonies during the winters of 1990–1991 and 1992–1993, respectively. We also collected 70 *macrogyna* colonies from 1990 to 1993. So far, gynandromorphs have been found among males from *microgyna* colonies and never among more than 1,000 males from *macrogyna* colonies. Therefore, our description of gynandromorphs is of the *microgyna* form.

Fifty-six of 124 (45.2%) colonies contained males. Gynandromorphs were found in 27 of 45 (60.0%) male-producing colonies examined. We studied the morphology and the frequency of gynandromorphs of only 21 colonies because 6 colonies were used for other studies. The total number of males examined was 779, among which gynandromorphs accounted for 16.9% (132 individuals). The radio of gynandromorphs to the total males in each colony varied from 3.7 to 47.7%, with an average of 21.4%.

The gynandromorphs were primarily male: all of them contained the male gaster. The female tissues occurred mostly in the head (99.2%), rarely in thorax (6.1%) and

Table 1. Frequency of body parts in which female tissues occurred among gynandromorphic males

Study area	Number of specimens	Head					Thorax	Petiole & post-petiole	Gaster
		Loss of ocellus	Compound eye	Antenna	Mandible	Other part			
Kaizu	105	26	31	26	40	102	5	1	0
Gifu	12	3	5	4	7	11	3	2	0
Kagamihara	15	2	4	4	9	14	0	0	0

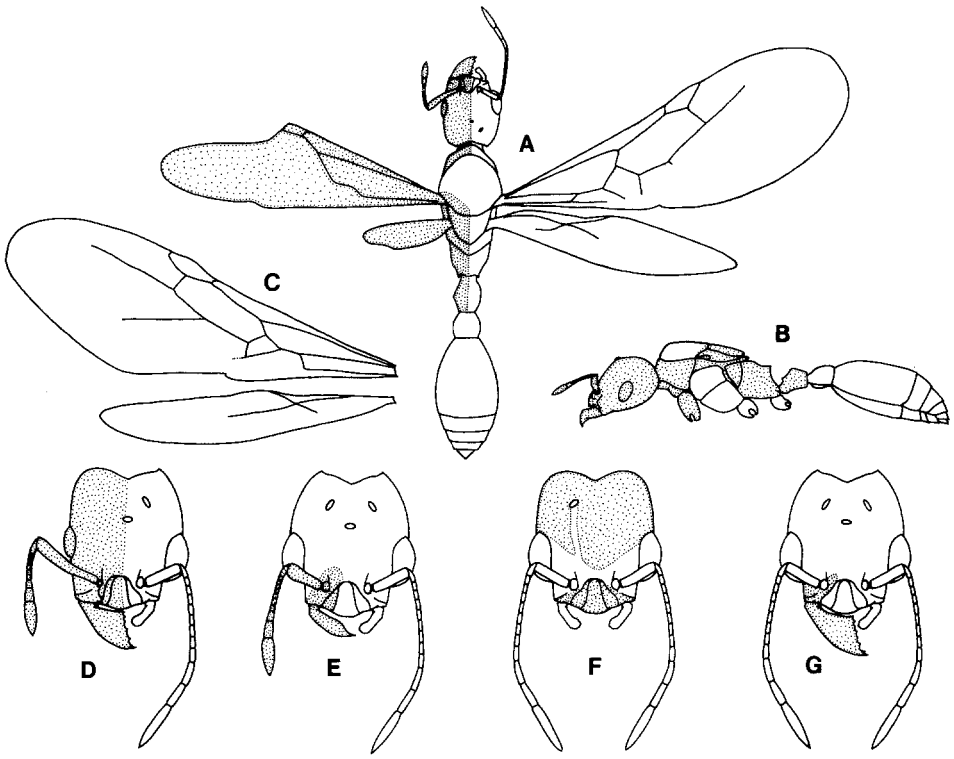

Figure 1. Some examples of gynandromorphs in *V. emeryi*. A, B: winged gynandromorph; C: normal wings of female; D–G: examples of head gynandromorphs; Dotted area: female tissue

very rarely in petiole and postpetiole (2.3 %) (Table 1). Moreover, female tissues were observed mostly on one side of the body (91.7 %; 47.9 % on the left side and 52.1 % on the right). On the other hand, queens and workers with masculized tissues were not found. Some examples of gynandromorphs are illustrated in Fig. 1. According to the nomenclature of Berndt and Kremer (1983), the majority of these individuals are androergatomorphs in the strict sense, because they have no ocellus on the female cuticle. We use the term gynandromorph here in a broad sense for simplicity.

The most remarkable gynandromorph exhibited a completely bilateral mosaic head: one side contained typical male characteristics (a long antenna with short

Figure 2. Scanning electron micrograph of a gynandromorphic head of a *V. emeryi*. male. Right half female, left male

scape, a large compound eye, distinct ocelli, and a small round mandible), whereas the other half contained typical female characteristics (a short antenna with long scape, a small compound eye, no ocellus, and a large denticulated mandible) (Fig. 2). The female cuticle was also easily recognized by brown patches that contrast with the black patches of males. Sculptures of cuticle and hairs on the cuticle of females are different from those of males (Fig. 2).

Gynandromorphs containing female tissues in the thorax were few. But fortunately, two individuals exhibited bisexual wings (Fig. 1). The left wings were female, but aberrant and short. However, these short wings are characteristic of the majority of *microgyna* queens.

Gynandromorphs were observed more frequently in micraner compared to macraner colonies, and never in macraners of *macrogyna* form. The frequency of gynandromorphs was 5.2% ($n = 158$) in macraner colonies and 20.0% ($n = 621$) in micraner colonies. The difference between micraner and macraner colonies was significant (χ^2-test, $P < 0.001$). Furthermore, the afore-mentioned winged gynandromorphs belong to macraner colonies (two specimens). Apparently "androergatomorphs" occur in micraners whereas "androgynomorphs" are found among macraners. *Vollenhovia emeryi* has a socially parasitic ant, *V. nipponica* (Kinomura and Yamauchi, 1992). In this study, 9 of 21 colonies exhibiting gynandromorphism contained the parasites. However, it seems that the parasites have no effect on gynandromorph formation, because gynandromorphs were found in many colonies without the parasites.

Discussion

The present study revealed that, in *V. emeryi* (*microgyna* form), 16.9% of males from the natural population contained partially feminized tissues. This high frequency of

gynandromorphism has never been reported in any ant species. Even in the experimental colonies of pharaoh's ant, in which gynandromorphs were induced by heat shock, the percent of gynandromorphism was 18.8% (Berndt and Kremer, 1982).

The presence of mosaic patterns suggests that abnormal cleavages took place during a limited period in early emblyogenesis and perhaps more than twice in some instances. However, the process of gynandromorph formation is unknown. Judging from the order of embryonic differentiation, all the gynandromorphs probably started as primarily male (all of them have a complete male gaster). Female tissues might be formed during relatively later stages by abnormal cleavages. A favored hypothesis is chromosomal non-disjunction (Taber and Francke, 1986), resulting in diploid cells which usually form female tissues in Hymenoptera. However, in this case, diploid chromosomes might be completely homozygous. According to a modern theory of haplodiploidy sex determination in Hymenoptera, such homozygosity may result in a male. Further studies are needed to know the mechanisms of gynandromorph formation.

To date, we have never observed mating behaviour in *microgyna*. However, inbreeding may frequently occur in this form because 1) the females cannot fly due to their short wings and 2) many inseminated winged females were found in the winter colonies. Inbreeding may preserve genetic factors which result in gynandromorphs because the males are taken care of by workers and they are relatively free from strict natural selection. Furthermore, it may be possible that gynandromorphism in this species might be caused by inbreeding depression. To clarify these problems, the mating system and the role of gynandromorphs in the system should be studied.

In conclusion, gynandromorphism occurs in all study areas that are more than 7 kilometers apart and throughout the study years, suggesting that gynandromorphism is not a rare phenomenon in *V. emeryi*. Therefore, this species may provide an opportunity for further studies on the morphogenesis of gynandromorphs and on their behavior.

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