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Queen polymorphism in an Australian ant, *Monomorium* cf. *rubriceps* MAYR, 1876 (Hymenoptera: Formicidae)

Alfred BUSCHINGER

Abstract

Queen polymorphism, the coexistence of two or more phenotypes of reproductive females in one species, is an uncommon feature in ants. In several ant species, queen polymorphism turned out to be genetically mediated. *Monomorium* cf. *rubriceps* MAYR, 1876 from south-eastern Australia is another species with workerlike, intermorphic queens but also alate / dealate ordinary gynomorphs. However, field and laboratory experiences suggest that this polymorphism is environmentally determined, in that a functional intermorphic queen inhibits the formation of alate gynomorphs in her progeny. Such gynes develop from her remaining brood when the queen has been removed or has died. Details of collecting sites, colony size and composition, reproductive organs and of the morphology of the reproductives are presented here. The author recommends further investigation of the phenomenon.

Key words: *Monomorium rubriceps*, queen polymorphism, genetic, environmental, caste determination, Australia.

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Prof. Dr. Alfred Buschinger, Rossbergring 18, D-64354 Reinheim, Germany. E-mail: hormigaleon.buschinger@t-online.de

Introduction

Most ant species have sterile workers and female reproductives with wings and a completely developed hymenopteran thorax. After mating, these females shed their wings and found colonies in one or the other way. In a comparatively high number of ant species, however, the female reproductives are wingless and have reduced thoracic structures making them somehow intermediate between the worker and the alate / dealate caste.

According to a morphological definition of castes, queens are the alate or dealate females, irrespective of whether they are mated and egg-laying, whereas the intermediates were dubbed intercastes, ergatoid queens, or gamergates. In a functional caste definition queens are the mated, egg-laying females that phenotypically may be gynomorphic (alate / dealate), intermorphic, or even workerlike (ergatomorphic). For reviews of these terminologies, see BUSCHINGER & HEINZE (1992) and HEINZE (1998, 2008).

Consequently, queen polymorphism means the coexistence of two or more morphologically different kinds of reproductive females within one species, though not necessarily together within a colony of this species. A number of instances have been listed in BUSCHINGER & HEINZE (1992). Among them are two Australian species, *Monomorium leae* FOREL, 1913 (= *Monomorium* sp. 10 in that paper) and *Monomorium* cf. *rubriceps* MAYR, 1876 (= *Monomorium* sp. 2).

In several ant species genetic mechanisms decide on whether a female larva can develop into a fully alate, or only into an intermorphic reproductive: *Harpagoxenus sublaevis* (NYLANDER, 1849) (WINTER & BUSCHINGER 1986), *Leptothorax* sp. A (HEINZE & BUSCHINGER 1989), *Myrmecina graminicola* (LATREILLE, 1802) (BUSCHINGER 2005), and probably *Monomorium leae* (see FERSCH & al. 2000).

Monomorium is a large and diverse genus in which "intercastes" or "ergatoids" have been reported for many species though usually the reproductive status of such intermorphs (morphologically between the worker and the alate / dealate gynomorph) has not been established (e.g., WHEELER 1917). In a couple of species an intermorphic form is the sole queen type, e.g., *Monomorium ergatogyna* WHEELER, 1904, and *Monomorium medinae* FOREL, 1892, the queen of which had been described as a social parasite under the name *Xenhyboma mystes* SANTSCHI, 1919 (ESPADALER 1982).

In contrast to the above-mentioned instances of genetically mediated queen polymorphism, *Monomorium* cf. *rubriceps* seems to represent a different, non-genetic mechanism of queen-morph determination. As was stated in BUSCHINGER & HEINZE (1992), all queenright field-collected colonies comprised a single intermorphic queen each, but after death or removal of this queen, the colonies reared several fully alate gynes from the remaining brood. Details of these observations shall be presented here.

Material and methods

The ants were collected in November 1987 and in March 1990 in Australia, New South Wales, in The Royal National Park and in the Blue Mountains. Table A1 (in Appendix, as digital supplementary material to this article, at the journal's web pages) presents the data of all 23 colonies that were detected during the two seasons. Numbers 13.xxx (14 colonies) were collected between 5 and 26 November 1987 at The Royal National Park (south of Sydney), and at Hampton State Forest / Jenolan Caves Road, Lithgow / Hassan's Walls and Hartley Vale (Blue Mountains). At that time in the southern spring, the colonies did

Tab. 1: *Monomorium* cf. *rubriceps*. Production of intermorphs (I) and gynomorphs (G) in laboratory culture (from BUSCHINGER & HEINZE 1992, adapted). * In BUSCHINGER & HEINZE (1992: table 2), this colony erroneously had the number 13.643.

Colony #	N intermorphs total	N intermorphs inseminated	N intermorphs egg-laying	Sexuals produced, comments
13.634*	11	?	?	I, and in last female brood, G
13.672	43	?	?	I, and in last female brood, G
14.283	10	1	1	I and G in first brood after de-queening
14.284	1	1	1 (old)	I and G in first brood after de-queening
14.296	6	1	1	I and G in first brood after de-queening

not yet comprise adult sexuals except for a couple of males that probably had hibernated in the nests. A few prepupae and worker pupae were present. Until the end of December 1987, most colonies that were kept alive had reared a number of pupae of intermorphs, workers and males. Numbers 14.xxx (nine colonies) were collected on 1 and 2 March 1990, with young males and intermorphic females, at Hampton State Forest / Jenolan Caves Road, Hartley Vale Pass and Lithgow / Hassan's Walls (Blue Mountains).

Nests were detected when flat slabs of ca. 10 to 30 cm diameter were removed from rocky outcrops in eucalypt forest. Colonies usually could be aspirated fairly completely from these nesting sites (Fig. 1).

The colonies were brought to Sydney, where they were checked for the presence of female reproductives, and a couple of specimens were dissected in the lab of Ross Crozier at the University of New South Wales, Kensington, NSW. Dissecting was done according to a standard technique (e.g., ALLOWAY & al. 1982).

Several colonies were brought alive to Germany where their offspring was reared and where experiments were run to breed the species. The colonies were kept in plastic boxes of variable sizes (dependent on colony size), with a bottom of plaster, in incubators at temperature regimes of 10°C for five months (hibernation), 10 / 20°C (daily rhythm, 12 / 12 hours) for three weeks in spring and in fall conditions, and 15 / 25°C (daily rhythm, 10 / 14 hours) for up to five months, depending upon brood development. The colonies always comprised numerous larvae during hibernation. Water, frozen mealworm pupae and honey-water (1:1) ad libitum were provided every second day except during hibernation where only honey and water was given once a week.

Fig. 1: *Monomorium* cf. *rubriceps*: nesting site in a rock cleft. The dark wall of detritus left to the tip of the handle of the axe had surrounded the colony. Blue Mountains, Hartley Vale, 1987.

Fig. 2: *Monomorium* cf. *rubriceps*: colony with intermorphic queen in the centre.

During several years of rearing under these conditions numerous offspring was reared including female (both intermorphic and gynomorphic, see below) and male sexuals. One colony, for example, was reared for six years from November 1987 until December 1993. However, it was not possible to observe successful mating, though futile mating attempts were frequently seen.

Results

Colony size varied considerably, from a few specimens (sometimes due to incomplete sampling) up to 43 intermorphs and up to 323 workers. Among the workers a variable fraction of larger workers could be distinguished, though worker size apparently varied continuously between the smallest and the largest that form a transition to intermorphs (Tab. A1, Fig. A5 in Appendix).

None of the 23 colonies collected in 1987 and 1990 comprised a dealate (gynomorphic) queen, and no young alate females or gynomorph pupae were recorded in the colonies when collected in the field. Intermorphic queens were identified in most of the colonies due to their physogastry (Fig. 2).

Dissections revealed that colonies may comprise multiple intermorphs (I), but are monogynous (Tab. 1). Five colonies had reared intermorphs. In laboratory culture later on, after one or more annual cycles, a number of alate

Fig. 3: *Monomorium* cf. *rubriceps*: dorsal view of (left) intermorph, (right) alate gynomorph, reared from a colony after the death of the intermorphic queen.

gynomorphs appeared always in their last female brood, after dequeening or loss of the original intermorphic queen (Fig. 3 and Figs. A3, A4 in Appendix). Queen loss was indicated by subsequent all-male broods.

Morphological inspection and dissections revealed that small and medium-sized workers don't possess ocelli, whereas large workers and intermorphs have one, two, or three ocelli. Gynomorphs always had three ocelli. The numbers of ovarioles were highly variable, between two in small workers and 19 in a gynomorph and 20 in an intermorph. The most frequent number in intermorphs was 12 ovarioles, six on either side. Gynomorphs and intermorphs possessed a spermatheca and a comparatively large bursa copulatrix. Sperm was found in the spermathecae of only one intermorph per colony, irrespective of the number of intermorphs present.

Discussion

This paper reports on somewhat preliminary observations and experiments that were run during work on another project, because by chance a couple of colonies of *Monomorium* cf. *rubriceps* with intermorphic queens were found. Nevertheless, this study yielded some very interesting results with respect to queen polymorphism in ants.

HETERICK (2001) provided a comprehensive description of *M. rubriceps* and its various subspecies, the (morphological) queen or gynomorph, the worker and the male. In "material examined" he mentions an "intercaste" of *M. rubriceps cinctum* WHEELER, 1917, and in "other material examined" several "ergatoids" which perhaps correspond to the "intermorphs" in the present paper. In the worker description, Heterick remarks "Worker caste monomorphic but variable in size, with series of intercastes between largest and smallest workers (monophasic allometry)." Under "queen description" we read: "Ergatoid or worker-female intercastes seen and examined." No details are given, however, on their morphological characters, e.g., of the ocelli which are clearly visible in the intermorphs as well as in the gynomorphs, and also their possible reproductive function is not mentioned.

WHEELER (1917) described and depicted a series of intermorphs of "*Monomorium rubriceps* MAYR var. *cinctum*". Ocelli are shown only on the head of a "dealated subapterous female", whereas worker and intermediates are represented solely by thoraces, and nothing is said on a reproductive function of the specimens.

Other data referred to in HETERICK (2001) do not well match the observations presented in this paper. So, colonies were reported to live in dead wood, in the ground or in vegetation. It was said that *M. rubriceps* occasionally may be a pest, found damaging Telecom cable junctions in Melbourne.

Having certain doubts on the identity of my material I therefore prefer to name it "*Monomorium* cf. *rubriceps*". More details and figures, including males (Figs. A1, A2) are provided in the Appendix. A couple of voucher specimens was sent to R.W. Taylor, Australian National Insect Collection, in February 1988.

According to HETERICK (2001) *Monomorium* cf. *rubriceps* belongs to a "*rubriceps* group of species" together with *Monomorium leae* (= *Monomorium* sp. 10 in BUSCHINGER & HEINZE 1992 and in FERSCH & al. 2000), where a genetically mediated queen polymorphism had been suggested.

For a species belonging to the species group of *Monomorium rothsteini* FOREL, 1902, BRIESE (1983) had described two different modes of reproductive behaviour, of two neighbouring and supposedly conspecific colonies. In one year, one of the colonies released winged males and females. The queens after swarming founded colonies nearby in the claustral manner. One year later the other colony released males and short-winged (brachypterous) gynes that mated on the nest. The mated queens then apparently returned into the mother colony which subsequently engaged in colony fission. Though an environmental influence (drought) was made responsible for the production of the brachypterous gynes in the second colony, it remains undetermined whether the two colonies in fact were conspecific, and whether the first colony had released any sexuals in the second year.

Since in the well established instances of genetically mediated queen polymorphism mentioned in the introduction the various queen morphs develop independently of the presence or absence of a functional queen, it is important here to emphasize that in *Monomorium* cf. *rubriceps* the mechanism is fundamentally different: There likely is no genetic difference among the female progeny of an intermorphic queen, but exclusively intermorphs were reared as long as the brood was under the influence of this queen, and alate gynes developed from her last brood in orphaned colonies. This mechanism somehow resembles the well-known phenomenon of queen inhibition, when only workers can develop in the presence of a functional queen, but gynes develop in the absence of this queen, or in distant parts of the nest. Several instances are reported in HÖLLDOBLER & WILSON (1990).

Further rearing and breeding *Monomorium* cf. *rubriceps* would be desirable to support this interpretation: No field colony has been found with a dealate gynomorph, hence nothing can be said on whether her reproductive offspring will be exclusively intermorphic, or gynomorphic, or both. I hypothesize that gynomorphs can make dispersal flights, found colonies independently, and thus may colonize distant localities, but direct evidence is lacking. So this paper is meant to recall this interesting feature and to encourage researchers in Australia to resume studies on queen polymorphism and its determining factors in *Mono-*

morium cf. *rubriceps*. Pictures in the Appendix may help to identify the species and to find colonies in the field.

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