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Hybrids in red wood ants (*Hymenoptera*, *Formicidae*)

[With 12 text-figures and 1 table]

Abstract. Among samples from 42 colonies of red wood ants that were analysed biometrically 2 were found to represent interspecific hybrids of *Formica polyctena* FOERST. \times *F. rufa* L. 3 phenotypes (*polyctena*-like, intermediate, *rufo*-like) were distinguished in both colonies; their quantitative proportion was almost identical, with predominance of the intermediate forms. The studies were conducted in the Gorce Mts. (the Western Carpathians) from 1985 to 1990.

INTRODUCTION

Cross-breeding is known to occur in ants. It has been recorded (usually under laboratory conditions) mainly in the family *Myrmicidae*: within the genera *Doronomyrmex* KUTTER (BUSHINGER 1972), *Leptothorax* MAYR (PLATEAUX 1976, 1977, 1978, 1979, 1981, 1987, SEIFERT 1984, HEINZE, BUSHINGER 1989), *Solenopsis* WESTW. (HUNG, VINSON 1977, ROSS et al. 1987), and *Epimyrma* EMERY (JESSEN, KLINKICHT 1990). PEARSON (1983) has recorded hybrids of *Lasius niger* (L.) \times *L. alienus* (FOERST). (*Formicidae*).

The subject of hybrids s often appeared in the literature on red wood ants (the *Formica rufa* group and the related species). This is the result of attempts to interpret the great and so far inexplicable individual variability of these ants and the presence of intermediate forms. These attempts followed two courses. The first (already abandoned) meant intricate development of the system and nomenclature (e.g., *F. rufa polyctena* var. *piniphila* ab. *pratensoides* FOREL, *F. rufa rufo-pratensis minor pratensoides* GÖSSWALD, *F. rufa pratensis nigricans* EMERY). The second course was made up of suppositions about cross-breeding and mixed colonies. The existence of mixed colonies already possesses docu-

mentary evidence – both for North American species (KING, SALLEE 1951) and for Euro-Siberian ones (CZECHOWSKI 1991a, b). In the case of hybrids, however, there is no explicit proof although successful (leading to insemination) cross-mating in the *F. rufa* group is a fact (GÖSSWALD 1960, GÖSSWALD, SCHMIDT 1960a, PAMILO et al. 1979).

FOREL (1874) wrote about intermediate forms meaning hybrids in red ants (among others). WASMANN (1915a, b, c) had no doubt they existed. He even made profound analyses of the principles of heredity (based on MENDEL's laws) using as an example colonies he considered to be hybrids of *F. rufa* L. × *F. pratensis* RETZ., *F. rufa* × *F. truncorum* FABR. and *F. truncorum* × *F. pratensis*. Those concepts were categorically rejected by YARROW (1955), and since that time the opinions on the possibility of the existence of hybrids have been more moderate. Even when morphological observations hinting at hybridization were supported by results of genetic studies (PAMILO, VEPSÄLÄINEN 1977, PAMILO et al. 1979).

New data on hybridization in red wood ants have been provided by biometric studies conducted by the Institute of Zoology, PAS on the material collected in the Gorce Mts. (the Western Beskidy) from 1985 to 1990.

RESULTS

The Gorce populations of *F. polyctena* FOERST. and *F. rufa* differ clearly in their ecological preferences and the structure of their societies (PISARSKI, CZECHOWSKI 1990), and also in the morphology of individuals (CZECHOWSKI 1991a, b, CZECHOWSKI, DOUWES, unpubl.). However, the analysed samples from 42 colonies that at first glance had been considered to be *F. polyctena* or *F. rufa* included samples from 2 colonies whose specificity could not be determined explicitly. These were Colonies U-III and U-IX, both monocalic ones, situated several hundred metres from each other, in the Jaszczce valley (the locality of Ochotnica Górna) at 780 (U-III) and 940 (U-IX) m above sea level in a habitat typical for *F. rufa* (PISARSKI, CZECHOWSKI 1990), among separate and dispersed nests of this species. In the vicinity there also were colonies, even polycalic ones, of *F. polyctena* (MABELIS 1988). The dimensions of the mounds of the colonies described were in 1985: U-III – $\Phi = 40$ cm, h = 20 cm; U-IX – $\Phi = 100$ cm, h = 60 cm, and in 1990: U-III – $\Phi = 90$ cm, ha = 30 cm; U-IX (after a removal) – $\Phi = 50$ cm, h = 30 cm.

The morphology of the red ants from the Gorce Mts. was analysed on the basis of the following characters of workers: colouration, size (width of the head and length of the thorax), pilosity (number of erect hairs on the bottom of the head, on the occiput and on the thorax). For Colonies U-III and U-IX the mean values of these characters (based on studies of 100 individuals collected from each colony in 1985) were on the whole very similar and generally placed them between *F. polyctena* and *F. rufa*. The average values of particular characters were closer to those typical of either one or the other species (Table 1). The variability distributions of the characters analysed in the colonies were significant.

Table 1. Morphometric characteristics (mean values) of workers from the Gorce populations of *F. polyctena* and *F. rufa* (after CZECHOWSKI 1991a) and from the colonies of interspecific hybrids: A – relative size of the dark spot on the alitrunk; B – width of the head (mm); C – length of the alitrunk (mm); numbers of standing hairs on: D – bottom of the head; E – occiput; F – alitrunk

Species		A	B	C	D	E	F
<i>F. polyctena</i>		4.44 ± 0.06	1.28 ± 0.02	2.13 ± 0.02	0.35 ± 0.07	0.45 ± 0.06	1.38 ± 0.17
<i>F. rufa</i>		3.76 ± 0.15	1.56 ± 0.02	2.56 ± 0.03	5.24 ± 0.34	2.83 ± 0.24	22.18 ± 1.01
Hybrids	U-III	4.15	1.40	2.36	1.63	2.01	10.16
	U-IX	4.48	1.52	2.44	1.51	1.86	9.68
	mean	4.32	1.46	2.40	1.57	1.94	9.92

The basic diagnostic characters of the red wood ants are connected with the pilosity of the bodies of workers. The variability distributions of these characters (pilosity of the, thorax the bottom of the head and the occiput) for Colonies U-III and U-IX appeared to be strikingly convergent (Figs 1–3), and statistically not different (χ^2 ; $P > 0.1$ in each case). Generalized results may therefore be used.

The pilosity of the thorax is the most spectacular character. The curves illustrating the distributions of its variability – both in either colony (Fig. 1) and in general (Fig. 4) – are distinctly three-part, three-peaked ones.

The course of the first part of the mean curve corresponds to the course of the analogous curve for *F. polyctena*. Individuals with hairless thoraces had the highest percentages in both cases (Fig. 4).

The inflexion point corresponding to 9 pairs of thorax hairs may be considered the beginning of the third part of the curve. This number (18 hairs) is (according to DLUSSKY and PISARSKI 1971) the borderline diagnostic character distinguishing *F. polyctena* from *F. rufa*. The course of this fragment of the curve corresponds to the top and descending part of the curve for *F. rufa*. Individuals with 11 pairs of hairs reached the highest percentage in both cases (Fig. 4).

The central part of the curve rises at the crossing point of the curves typical for *F. polyctena* and *F. rufa*. Its top corresponds to a class of individuals with 5 pairs of thorax hairs. This is almost precisely the mean value for the pilosity of the Gorce *F. polyctena* and *F. rufa* (Fig. 4)

The distribution presented here shows that the colonies under discussion consisted of 3 morphologically separate (in respect of the pilosity of the thorax) groups of individuals: 1) forms corresponding to *F. polyctena*, 2) intermediate forms, 3) forms corresponding to *F. rufa*.

The shares of these groups, estimated directly on the basis of the course of the curve analysed, are as follows: *polyctena*-like forms (0–1 pair) – 20%, intermediate forms (2–8 pairs) – 64%, *rufa*-like forms (≥ 9 pairs of hairs on the thorax) – 16%. However, this is not precise estimation because the ranges of the individual variability of the red ants overlap. In the Gorce Mts. about 20% workers in the population of *F. polyctena* have more than 1 pair of hairs on the thorax, and 32% is the population of *F. rufa* do not reach the diagnostic minimum

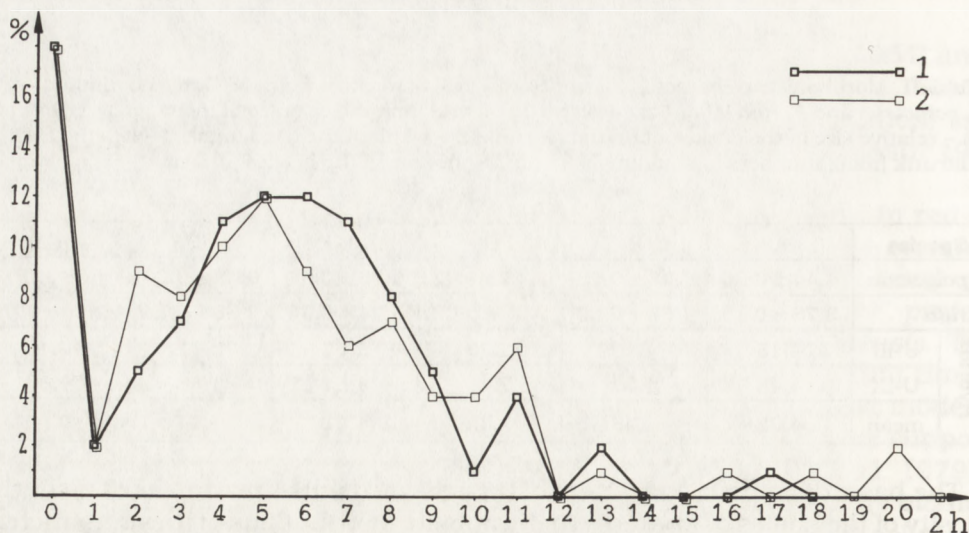


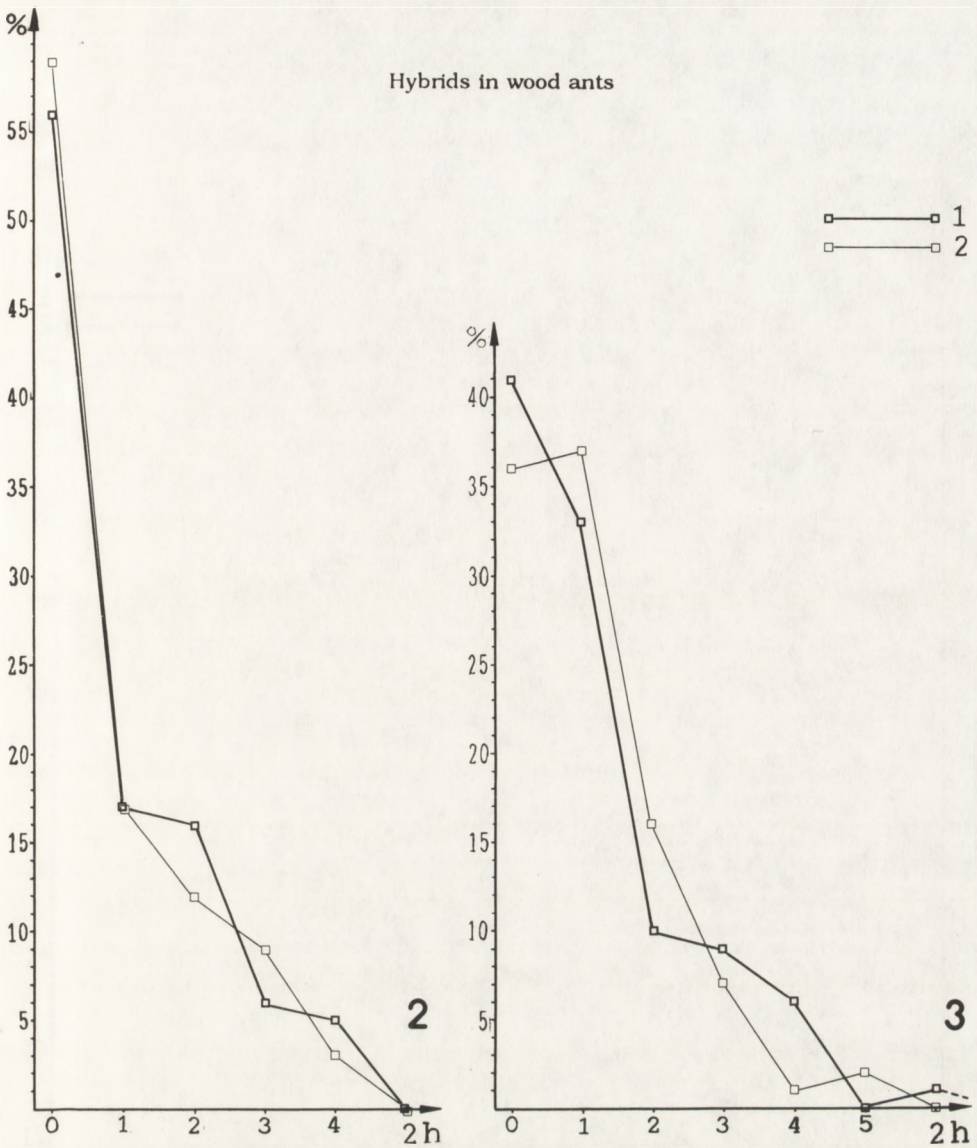
Fig. 1. Variability distribution of the pilosity of the thorax in workers from Colonies U-III (1) and U-IX (2) (2h – number of pairs of hairs).

of 18 hairs (CZECHOWSKI 1991b). Such individuals (very hairy *F. polyctena* and poorly hairy *F. rufa*) may artificially overstate the percentage of the intermediate forms in Colonies U-III and U-IX. With this in mind, the real percentage of particular forms may be considered as close to 1:2:1.

In *F. polyctena* and *F. rufa* the pilosity of the bottom of the head and of the occiput is closely positively correlated with the pilosity of the thorax ($r = 0.95$ and 0.87 , respectively; $n = 49$; CZECHOWSKI, DOUWES, unpubl.). The values of the individual variability coefficient ($v = SD/\bar{x} \times 100\%$) of these characters in the Gorce populations are much higher than the analogous value for the pilosity of the thorax (CZECHOWSKI 1991a). This great variability is responsible for the fact that the diagrams illustrating the variability distribution of both characters in Colonies U-III and U-IX do not show very clearly the heterogeneity (triplicity) of the swarms (Figs 2, 3). But they show very well the intermediate type of these colonies in relation to *F. polyctena* and *F. rufa* (Figs 5, 6).

Workers from Colonies U-III and U-IX were dark. In respect of colouration (the dark spot on the thorax) most individuals belonged to Classes 4 and 5 (according to the 6-degree scale of GÖSSWALD and SCHMIDT 1960b) (Fig. 7). This resulted in high mean values close to those typical for *F. polyctena* (Table 1). The variability distribution of this character (for both colonies together) is almost the same as that for the population of *F. polyctena* (Fig. 8). In the red ants the (negative) correlation between the colouration of the thorax and its pilosity is fairly significant ($r = -0.52$; CZECHOWSKI, DOUWES, unpubl.). It was logical therefore, to expect a more even distribution of the variability of this character. Yet colouration, which is conditioned to some extent by environmental factors (PISARSKI 1981), cannot be considered a good diagnostic character.

The same applies to the size of the body. It is true that in the red ants the correlation between the width of the head and the length of the thorax and the



Figs 2 and 3. Variability distributions of the pilosity of the bottom of the head (Fig. 2) and the occiput (Fig. 3) in workers from Colonies U-III and U-IX (symbols as in Fig. 1).

pilosity of the thorax is high ($r = 0.65$ and 0.82 , respectively; CZECHOWSKI, DOUWES, unpubl.), but it should be ascribed more to coincidence than to the linkage of characters. The size of workers (and its differentiation within a given swarm) depends on the intensity with which larvae are fed, and this in turn depends on the trophic abundance of the habitat, but also on the age and the social structure of the colony (PISARSKI 1973, 1981, 1982, PISARSKI, BANERT 1982).

On average, workers from U-III were almost exactly of the medium size in relation to *F. polycytena* and *F. rufa*. Ants from U-IX were bigger, their size was closer to that of *F. rufa* (Table 1). In both cases the intracolony differentiation in size was very small (Figs 9–12).

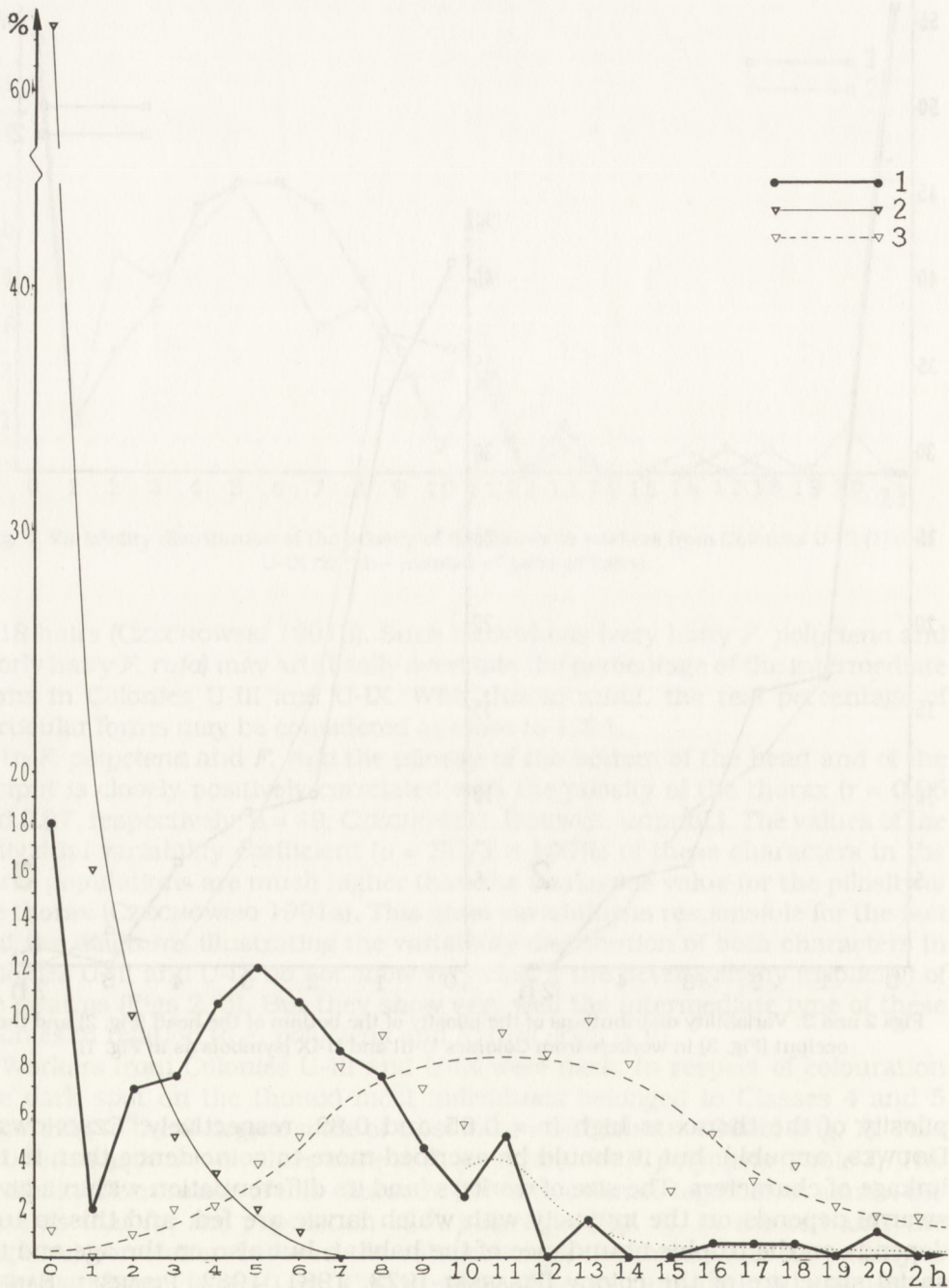
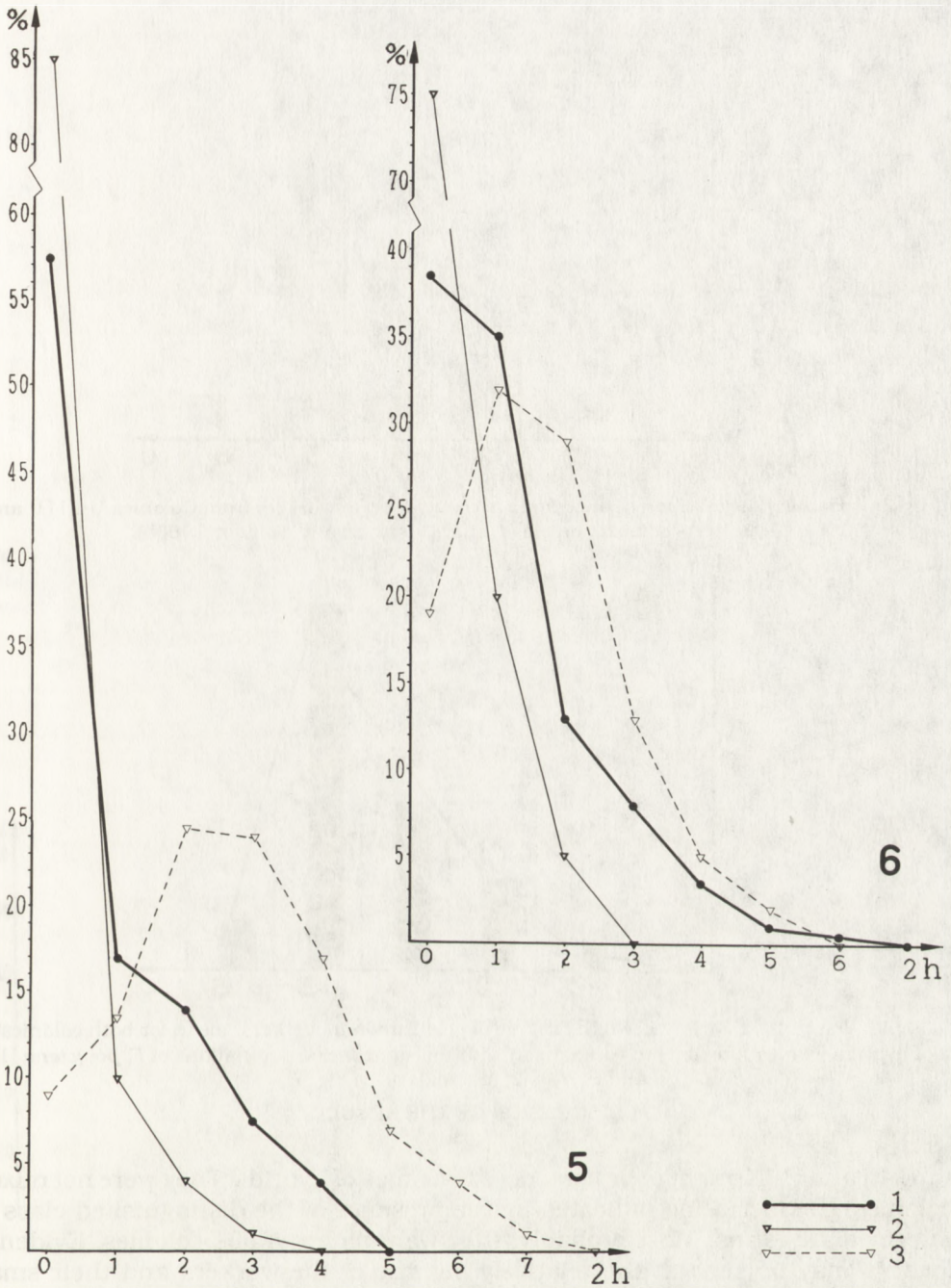


Fig. 4. Variability distribution of the pilosity of the thorax in workers, mean for both colonies of hybrids (1), in comparison with the same in the populations of *F. polyctena* (2) and *F. rufa* (3) (2h - number of pairs of hairs). [Material compared (applies to the following figures as well): *F. polyctena* - 30 individuals from each of the 31 colonies; *F. rufa* - 30 individuals from each of the 11 colonies].



Figs 5 and 6. Variability distributions of the pilosity of the bottom of the head (Fig. 5) and the occiput (Fig. 6) in workers, mean for both colonies of hybrids, in comparison with the same in the populations of *F. polycтена* and *F. rufa* (symbols as in Fig. 4).

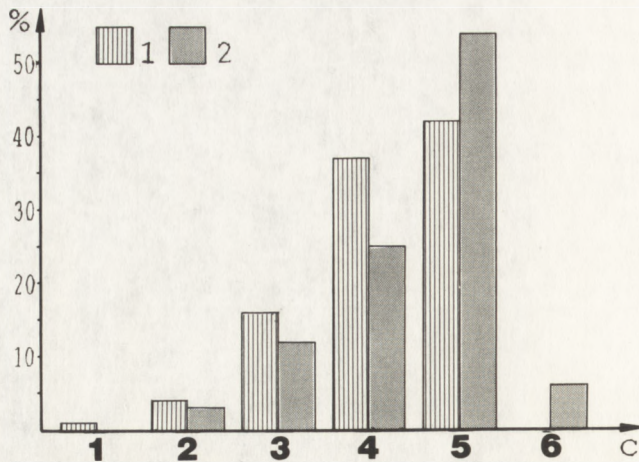


Fig. 7. Variability distribution of the degree of colouration in workers from Colonies U-III (1) and U-IX (2) (c - colouration class, after GÖSSWALD and SCHMIDT 1960b).

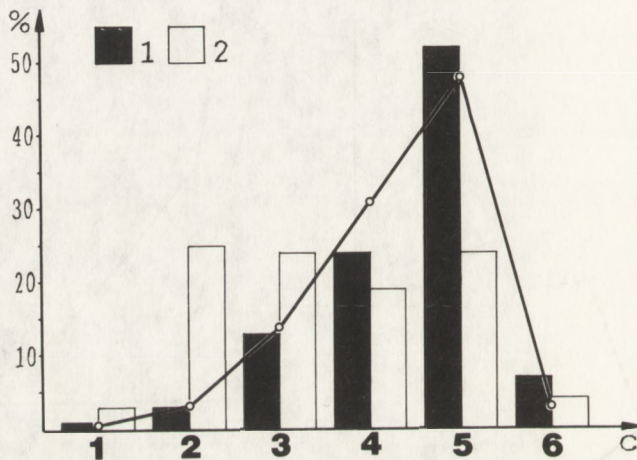


Fig. 8. Variability distribution of the degree of colouration in workers, mean for both colonies of hybrids (continuous line) in comparison with the same in the populations of *F. polyctena* (1) and *F. rufa* (2) (c - scale as in Fig. 7).

DISCUSSION OF THE RESULTS

U-III and U-IX ought to be considered colonies of hybrids. They were not mixed colonies, the fact being indicated by the presence of the distinguished class of intermediate forms. Most probably, they were monogynous colonies. Evidence for this may be seen in the relatively big size of the workers and their small differentiation in this respect, and also in the aggressiveness of individuals in intercolonial relations. Moreover, during the five seasons of studies no inclination to perform colony fission was observed in the colonies.

The principles on which the morphological characters discussed here are inherited are as yet not known (monogenic heredity, multiple alleles?). The

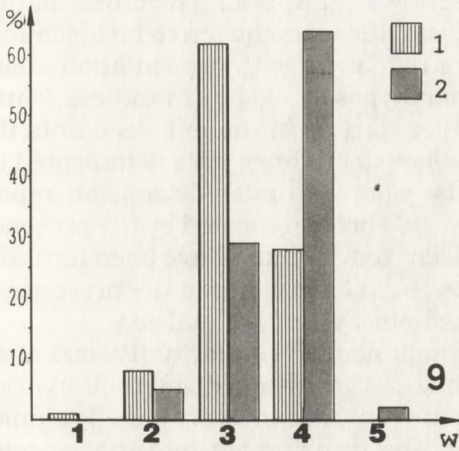


Fig. 9. Variability distributions of the width of the head in workers from Colonies U-III (1) and U-IX (2) [w - scale (in mm): 1 - 0.6-0.8, 2 - 0.9-1.1, 3 - 1.2-1.4, 4 - 1.5-1.7, 5 - 1.8-2.01].

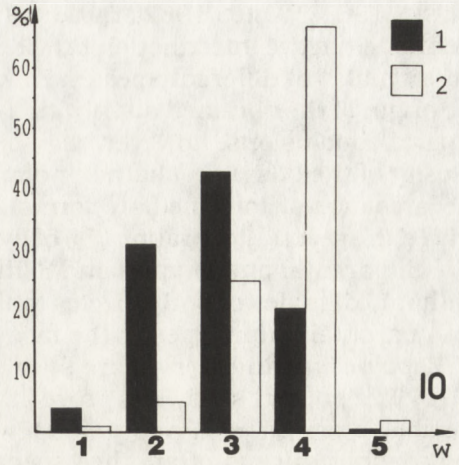


Fig. 10. Variability distributions of the width of the head in workers from the populations of *F. polyctena* (1) and *F. rufa* (2) (w - scale as in Fig. 9).

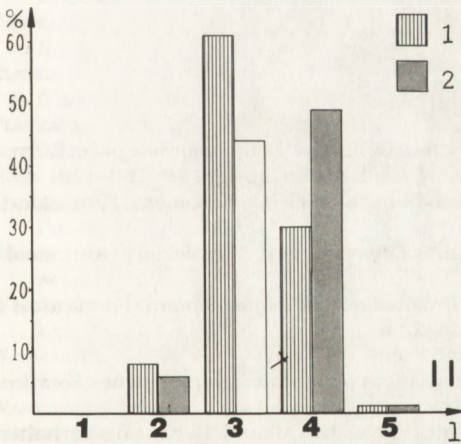


Fig. 11. Variability distributions of the length of the thorax in workers from Colonies U-III (1) and U-IX (2) [l - scale (in mm): 1 - 1.0-1.4, 2 - 1.5-1.9, 3 - 2.0-2.4, 4 - 2.5-2.9, 5 - 3.0-3.4].

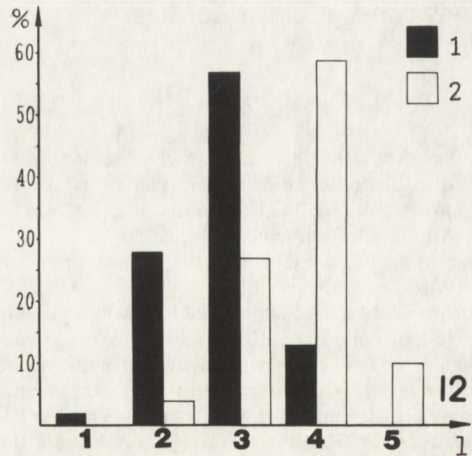


Fig. 12. Variability distributions of the length of the thorax in workers from the populations of *F. polyctena* (1) and *F. rufa* (2) (l - scale as in Fig. 11).

situation is further complicated by the polyandry of queens of red ants (MARIKOVSKY 1961, PAMILO 1982, YAMAUCHI, CZECHOWSKI, unpubl.). The cross-mating mentioned in the introduction provides possibilities for a queen to be inseminated by males of different species. In view of this any lengthy speculation about the origin of the obtained distribution of phenotypes would be groundless. Three general conclusions, however, may be put forward: 1) in the red wood ants the pilosity of the body is a character of incomplete dominance (this is indicated by the presence of intermediate forms), 2) the colonies under discussion represented the second generation (F₂) of hybrids (this being indicated by the presence of both parental phenotypes) and 3) the queen from F₁ must have been fertilized by (haploid) males of both species (only this could have ensured the presence of both parental phenotypes in the face of the homozygosity of males).

F. polyctena and *F. rufa* are species of high genetic similarity (PAMILO et al. 1979). The present study has proved that they can cross-breed and their hybrids are able to reproduce. Prior to that it was found out that their orphaned colonies could adopt queens of another species and be transformed into that species (CZECHOWSKI 1991a) or, by simultaneous adoption of queens of both species, they could become permanently mixed colonies (CZECHOWSKI 1991b). Certain data (PAMILO, VEPSÄLÄINEN 1977, PAMILO et al. 1979, VEPSÄLÄINEN, PISARSKI 1981) suggest that similar phenomena may occur also in other pairs of species of red wood ants (*F. polyctena*/*F. aquilonia* YARR., *F. rufa*/*F. lugubris* ZETT.). The situation is best expressed by the title of an article by VEPSÄLÄINEN and PISARSKI (1981): "The taxonomy of the *Formica rufa* Group: Chaos before Order" – devoted to controversies between the currently accepted (hitherto existing?) taxonomic system of the subgenus *Formica* s. str. and the universally recognized (up till now?) concept of the species.

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STRESZCZENIE

[Tytuł: Mieszzańce międzygatunkowe rudych mrówek leśnych (*Hymenoptera*, *Formicidae*)]

Wśród przeanalizowanych biometrycznie prób z 42 mrowisk gatunków z grupy *Formica rufa*, zebranych w Gorcach (Beskidy Zach.) w latach 1985-1990, dwie reprezentowały mieszańce międzygatunkowe *F. rufa* × *F. polyctena* FOERST. Pod względem oszczecenia ciała (podstawowej cechy diagnostycznej mrówek rudych) w obu mrowiskach były wyodrębnione 3 fenotypy (obie formy rodzicielskie i forma pośrednia), występujące w niemal identycznym stosunku ilościowym (z przewagą form pośrednich). Pod względem ubarwienia hybrydy były zbliżone do *F. polyctena*, a pod względem wielkości do *F. rufa*. Nietypowe mrowiska określono jako reprezentujące drugie pokolenie (F₂) mieszańców, powstałe w wyniku zapłodnienia samicy z F₁ przez samce obu gatunków rodzicielskich.