

# PSYCHE

---

Vol. 102

1995

No. 1-2

---

## QUEEN SIZE VARIATION IN THE PONERINE ANT *PONERA COARCTATA* (HYMENOPTERA: FORMICIDAE)

BY J. LIEBIG, J. HEINZE, AND B. HÖLLDOBLER

Theodor-Boveri-Institut,  
LS Verhaltensphysiologie und Soziobiologie,  
Am Hubland, D-97074 Würzburg, Germany

### ABSTRACT

Queens of *Ponera coarctata* show a pronounced variation in size as measured by ommatidia number and Weber's alitrunk length. Isometric size variation and the normal distribution of size categories indicate that, despite these differences, only one queen morph exists. Queen size varies less within colonies than between colonies, and thus appears to be colony specific. Ovary length apparently varies with queen size. Similar size variations as in queens also occurred in males, but not in workers.

### INTRODUCTION

In the majority of ant species female reproductives show the typical alitrunk of a hymenopteran female, i.e., fully developed thoracic sclerites and wings, which are shed after mating. Alternatively, the normal, originally winged queens may be replaced by wingless (apterous) reproductives with a more or less greatly reduced alitrunk structure (intercastes and ergatoid queens sensu Peeters, 1991), and rarely two or more reproductive morphs may

---

*Manuscript received 3 March 1995.*

co-occur within a single species (see Peeters, 1991 and Buschinger and Heinze, 1992, for examples).

Several authors have suggested that ecological factors underlie or cause aberrant queen morphology (e.g., Bolton, 1986; Villet, 1989; Heinze, 1989, 1993; Tinaut and Heinze, 1992). An analysis of the initial stages of queen morph variation might contribute to a better understanding of the evolution and the ecological significance of this phenomenon. These initial stages might be represented by species where queen size is variable without pronounced differences in morphology.

We here describe a remarkable example of such size variation in queens of the palearctic ponerine ant *Ponera coarctata*.

#### MATERIAL AND METHODS

Colonies of *Ponera coarctata* were collected in July and August 1992, and between April and September 1993 in the vicinity of Würzburg, Bavaria, Germany. Colonies rarely exceeded 60 workers. The largest was collected at the end of July 1992, and contained two queens, 135 workers, 238 cocoons, and 23 larvae. Colonies collected in the fall contained alate queens and males or pupae of sexuals. Colonies were kept in the laboratory (day-night rhythm: 13hr at 25°C (8:00 to 21:00) and 11hr at 15°C (21:00 to 8:00)) until the eclosion of sexuals. In two colonies (C and D), queens were produced in the laboratory. Colonies F, H, I, and K were collected without reproductive queens. The following measurements were made using a binocular microscope at 25×–40× magnification: Weber's length (WL), the distance from the pronotal margin, excluding its frontal collar, to the posterior margin of the propodeum, measured in lateral view, maximum head width in frontal view (workers and queens: excluding eyes, males: including and across eyes), maximum scutum width and length in dorsal view, maximum wing length, egg size, and ovary length. The number of ommatidia was counted on SEM-micrographs. The ants were dissected in Ringer's solution by carefully removing the gastric tergites and the fat body until the ovaries were visible.

#### RESULTS

The examination of 79 queens of *Ponera coarctata* from 11 colonies revealed pronounced size variation (Tab. 1). The alitrunks

Table 1: Size variation of sexuals and workers in the ant *Ponera coarctata*, lengths in mm (precision:  $\pm 0.01$ mm). Wing lengths are average lengths of both wings when both were present, ommatidia number refers to one eye, n = sample size,  $\bar{X}$  = arithmetic mean, SD = standard deviation.

	n	$\bar{X} \pm SD$	Range
<b>Queens</b>			
Number of ommatidia	75	109 $\pm$ 19	59 - 149
Head width	35	0.64 $\pm$ 0.02	0.59 - 0.68
Weber's alitrunk length	77	1.17 $\pm$ 0.06	1.01 - 1.3
Scutum width	75	0.49 $\pm$ 0.04	0.42 - 0.58
Scutum length	75	0.36 $\pm$ 0.02	0.3 - 0.42
Wing length			
Forewing	24	2.68 $\pm$ 0.18	2.22 - 2.95
Hindwing	14	2.04 $\pm$ 0.14	1.79 - 2.27
<b>Males</b>			
Weber's alitrunk length	49	1.14 $\pm$ 0.06	0.97 - 1.28
Head width	49	0.61 $\pm$ 0.03	0.54 - 0.68
<b>Workers</b>			
Number of ommatidia	25	3.8 $\pm$ 1.4	1 - 7
Weber's alitrunk length	20	0.98 $\pm$ 0.03	0.92 - 1.02
Head width	20	0.58 $\pm$ 0.02	0.56 - 0.62

of the largest queens were some 30% longer than those of the smallest queens. Scutum measurements showed even more variation: the scutum of the largest queen (0.58mm) was almost 38%

wider and 40% longer than that of the smallest queen. Queen head width differed by up to 15%. The number of ommatidia per compound eye also varied remarkably (Fig. 1): the eye of the largest queen consisted of almost 250% more ommatidia (149 omm.) than that of the smallest queen (59 omm.).

Size varied continuously: the frequency distributions of queens in different size classes or with different ommatidia numbers were normally distributed (Fig. 2, Chi-Square test,  $X^2 = 1.51$ ,  $df = 4$ ,  $p = 0.82$  and  $X^2 = 2.60$ ,  $df = 3$  and  $p = 0.46$ , respectively).

Alitrunk length (WL) of queens and ommatidia number were correlated (Pearson product-moment,  $n = 66$ ,  $r = 0.77$ ,  $p < 0.0001$ , Fig. 3). The size variation of queens within each of eight colonies was characterized by individual regression lines. Intracolony size variation was always restricted to a certain range of the total variation. The differences in queen sizes between colonies were statistically significant (Single classification ANOVA for alitrunk length,  $F = 23.1$ ,  $p < 0.0001$ ) whereas the variances of colonies did not differ significantly (Bartlett's test,  $p > 0.21$ ). In colony A, the ommatidia number of 14 a total of 16 queens ranged between 83 and 101; the two remaining queens had 69 and 119 ommatidia, respectively, causing an extraordinarily high intracolony variation. Wing length was also correlated with alitrunk length (Pearson

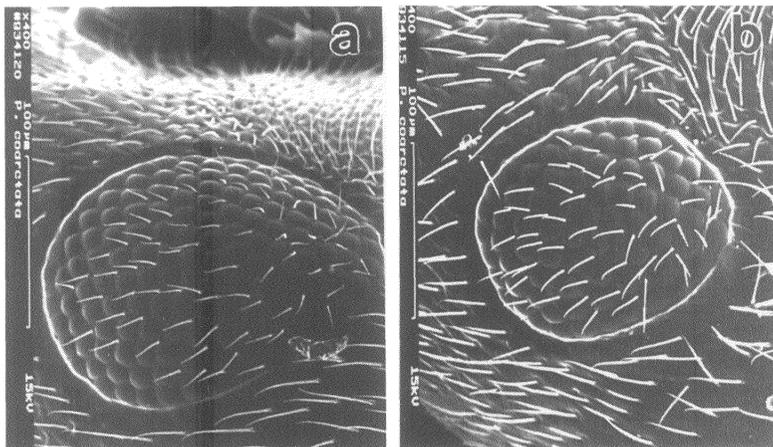


Fig. 1: Compound eye of a) a large queen and b) a small queen of the ant *Ponera coarctata*.

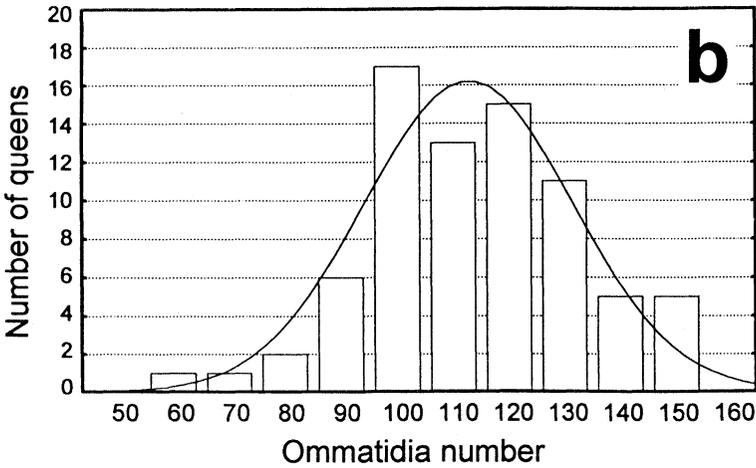
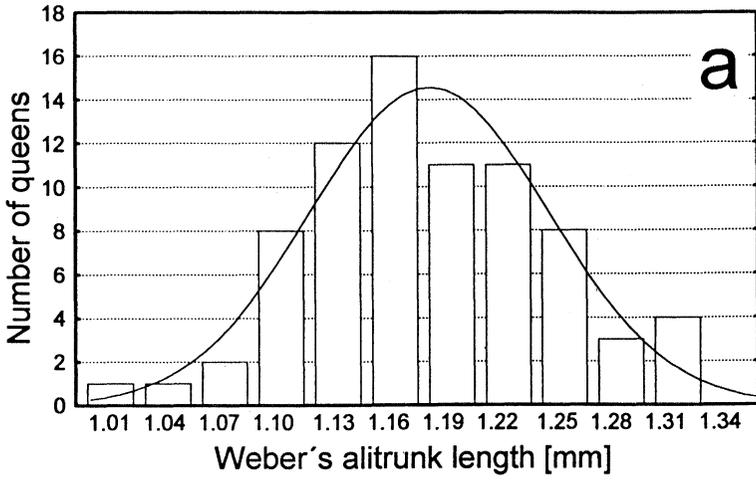


Fig. 2: Size distribution of queens of *Ponera coarctata*. Category width is a) 0.03mm for WL (n = 77) and b) 10 ommatidia for the number of ommatidia per eye (n = 76). Numbers refer to the upper limit of the categories. The superimposed curve indicates a normal distribution fitted to the histograms.

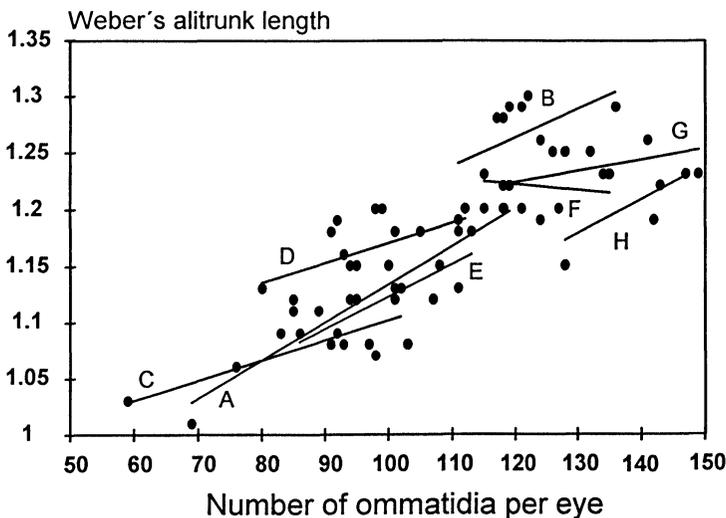


Fig. 3: Relation between WL and ommatidia number in queens of *Ponera coarctata*. The letters with corresponding regression lines represent the size spectrum within single colonies. End points of regression lines represent the ommatidia number of the smallest and the largest queen of that colony, respectively. Colony A:  $n = 16$ , B:  $n = 8$ , C:  $n = 4$ , D:  $n = 13$ , E:  $n = 6$ , F:  $n = 7$ , G:  $n = 7$ , H:  $n = 5$ .

product-moment,  $n = 24$ ,  $r = 0.87$ ,  $p < 0.0001$ ). Here, too, none of the four colonies with winged queens contained alates with wing lengths varying over the total range.

A comparison of the ratios scutum length/WL and scutum width/WL with WL showed that alitrunk proportions do not change with increasing queen size (Fig. 4). This was also evident from examination of the alitrunks of a large queen, a small queen, and a worker (Fig. 5). Despite the large size differences between the two queens, the morphology of their alitrunks was almost identical, i.e., small queens are almost isometrically reduced variants of large queens. Intercastes or ergatoid queens were not found.

Queens of all sizes were inseminated and were observed laying eggs. The ovary of queens and workers invariably consisted of two sets of three ovarioles, but workers lack a spermatheca. The presence of visible ovaries in workers was apparently independent of age, in contrast to, e.g., *Hypoponera* sp., where young workers

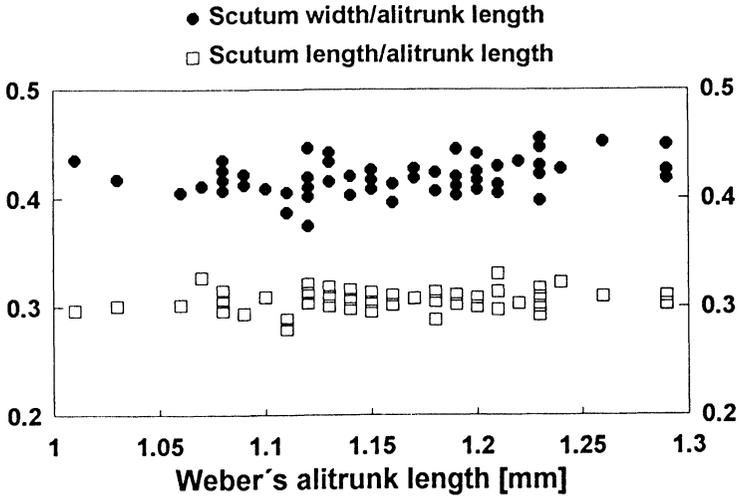


Fig. 4: Size relation between scutum and alitrunk length in queens.

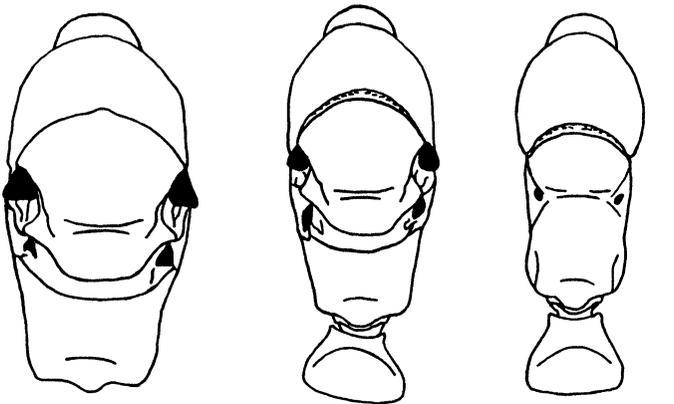


Fig. 5: Alitrunk morphology of a large queen, a small queen, and a worker in dorsal view. The petiole is included in the small queen and the worker. The large and the small queens' alitrunk had a length (WL) of 1.31mm and 1.08mm, respectively. The scale equals 0.5 mm.

were observed laying eggs in orphaned colonies, but in older workers their two single ovarioles became completely resorbed (unpublished observations). Ovarioles were obviously longer in queens than in workers of *P. coarctata*. The average maximum ovary length of queens with no more than a single large yolky oocyte and a few small oocytes was 2.0mm (SD 0.28mm,  $n = 6$ ), whereas worker ovaries with at least one yolky oocyte measured 0.8mm (mean, SD 0.15mm,  $n = 24$ ). In five dissected queens, both alitrunk length and ovariole length were measured. The largest queen (1.24mm WL) had an ovariole length of 2.32mm, two large queens (1.22mm and 1.22mm WL) had an ovariole length of 2.06mm, whereas the ovaries of two small queens (1.11mm and 1.06mm WL) were each 1.68mm long. Ovariole size did not influence egg size. Queens and workers laid eggs of similar size (15 queen eggs: length  $0.71 \pm 0.05$ mm, width  $0.27 \pm 0.01$ mm; 24 worker eggs: length:  $0.71 \pm 0.04$ , width:  $0.27 \pm 0.02$ mm).

Measurements of 49 males revealed similar size variation as in queens (Tab. 1). The alitrunk of the largest male was 32% longer than that of the smallest male. Alitrunk length and head width were positively correlated (Pearson product-moment,  $n = 49$ ,  $r = 0.79$ ,  $p < 0.0001$ ). The size distribution of males was not as colony specific as that of queens (Fig. 6). Only colony L, which contained the two smallest males, differed conspicuously in terms of male size variation from other colonies. In contrast to queens and males, workers of *P. coarctata* varied less in size (Tab. 1).

#### DISCUSSION

In a number of ant species, female reproductives differ markedly in size and frequently also in the development of wings, ocelli, and thoracic structure (Peeters, 1991; Buschinger and Heinze, 1992). We document here considerable size variation in queens of the palearctic ponerine ant *Ponera coarctata*, where the alitrunk of the largest queens is about 30% longer and about 40% wider than that of the smallest queens. Although the consequences of this variation are unknown, body size apparently affects the length of the queens' ovarioles. Because eggs laid by small and large queens are of similar size, one important consequence of smaller queen size might be a decrease in fecundity (see also Villet, 1990).

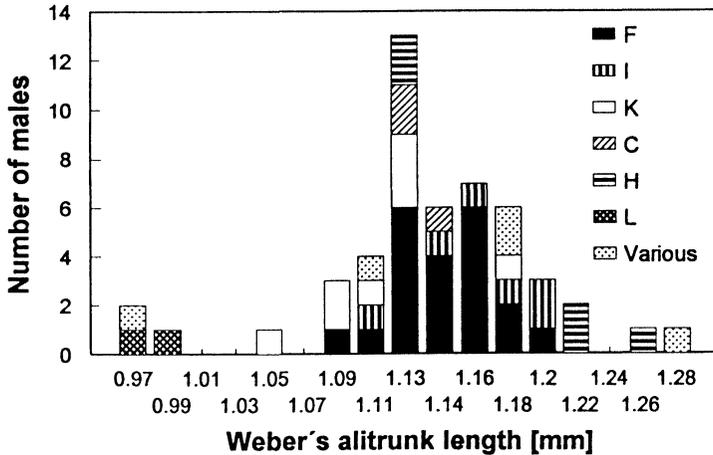


Fig. 6: Sizes of males of different colonies of *Ponera coarctata*.

Despite large size differences, small and large queens are almost identical in the structure of their alitrunks. Though Stitz (1939) mentioned ergatoid queens in *P. coarctata*, all queens in our sample had a complete set of thoracic sclerites and bore wing remnants. Similar queen size variation is known in *Myrmica ruginodis* (Brian and Brian, 1949; Elmes, 1991) and *Pseudomyrmex venefica* (Janzen, 1973). In *Polyrhachis* cf. *doddi* size variation is associated with a more or less allometric reduction in scutum size (Heinze and Hölldobler, 1993). The size distribution of *P. coarctata* queens is continuous rather than bimodal. It is therefore not useful to refer to distinct queen morphs (macro- and microgynes) in this species, as was done by Stitz (1939) and is common usage in the *Myrmica* literature.

Queens reared within a single colony typically differ less markedly from each other than queens taken at random from the population, though colonies apparently do not specialize in producing only small or only large queens. Whether size variation is caused by genetical or environmental factors is not known. In two queen-polymorphic leptothoracines, *Harpagoxenus sublaevis* and *Leptothorax* sp. A, the queen morph is genetically determined, but environmental or social control appears more likely in this species (Buschinger and Heinze, 1992). Some of the smallest queens of *P.*

*coarctata* in our sample were reared under artificial conditions in incubators; this might suggest a strong environmental influence. On the other hand, only queens and males showed considerable size variation, whereas workers varied much less.

Queen polymorphism in ants, as well as wing dimorphism in other insects, is thought to be correlated with alternative dispersal strategies (Buschinger and Heinze, 1992; Tinaut and Heinze, 1992). For example, in *Myrmica ruginodis*, *Pseudomyrmex venefica*, and *Polyrhachis* cf. *doddi* it has been suggested that large queens disperse and colonize new habitat patches, whereas small queens tend to re-enter the maternal nest (Elmes, 1991; Janzen, 1973; Heinze and Hölldobler, 1993). Similarly, according to field and laboratory observations, winged queens of *Leptothorax* sp. A usually disperse and found new nests solitarily, whereas wingless "intermorphic" queens mate in the immediate neighborhood of the maternal nest and return to it for hibernation (Heinze, 1989; 1993). Whether size variation is correlated with alternative dispersal and founding strategies in *P. coarctata* is not yet clear. Large queens were observed flying and we assume that small queens are also capable of flight because of their similar alitrunk structure. Queen readoption might play a role in *Ponera pennsylvanica*, the sister species of *P. coarctata* (Taylor, 1967), where apterous queens occur regularly (Pratt, Carlin, and Calabi, 1994). We did not find apterous queens in *P. coarctata*, although its ecology is quite similar to that of *P. pennsylvanica*. However, in 5 of a total of 17 collected queenright colonies, multiple queens were present, thus indicating that either pleometrosis or adoption might be a common phenomenon. A more detailed examination of the life histories of small and large queens in this species might help to understand the evolution of the more pronounced queen polymorphism observed in other ant species.

Another subject for future investigation is the enormous variation in the number of ommatidia. Similar variation has been described for workers of *Cataglyphis bicolor* (Menzel and Wehner, 1970), *Formica integroides* (Bernstein and Finn, 1971), and *Camponotus pennsylvanicus* (Klotz, Reid, and Gordon, 1992), and further analyses will probably document similar correlation between eye and body size in other species. Although experiments revealed that differences in eye size are associated with different ethotypes

and different visual orientation ability in workers of *Formica integroides* (Bernstein and Bernstein, 1969) and *Cataglyphis bicolor* (Wehner and Menzel, 1969; Menzel and Wehner, 1970), the significance and the consequences of eye size variation in queens of *P. coarctata* are unknown.

#### ACKNOWLEDGEMENTS

We thank two anonymous referees for useful comments on the manuscript and Stephen Pratt for sending some specimens of *Ponera pennsylvanica*. This work was supported by DFG-funds (Leibniz-Prize to B. Hölldobler).

#### LITERATURE CITED

- Bernstein, S., and R.A. Bernstein. 1969. Relationships between foraging efficiency and the size of the head and component brain and sensory structures in the red wood ant. *Brain Res.* 16:85–104.
- Bernstein, S., and C. Finn. 1971. Ant compound eye: size related ommatidium differences within single wood ant nest. *Experientia* 27 708–710.
- Bolton, B. 1986. Apterous females and shift of dispersal strategy in the *Monomorium salomonis*-group (Hymenoptera: Formicidae). *J. Nat. Hist.* 20:267–272.
- Brian, M.V., and A.D. Brian. 1949. Observations on the taxonomy of the ants *Myrmica rubra* L. and *M. laevinodis* Nylander (Hymenoptera: Formicidae). *Trans. R. Ent. Soc. Lond.* 100 (14): 393–409.
- Buschinger, A., and J. Heinze. 1992. Polymorphism of female reproductives in ants. In: Billen, J. (ed.) *Biology and evolution of social insects*. Leuven University Press, Leuven, 11–23.
- Elmes, G.W. 1991. Mating strategy and isolation between the two forms, macrogyna and microgyna, of *Myrmica ruginodis* (Hym. Formicidae). *Ecol. Entomol.* 16:411–423.
- Heinze, J. 1989. Alternative dispersal strategies in a North American ant. *Naturwissenschaften* 76:477–478.
- \_\_\_\_\_. 1993. Habitat structure, dispersal strategies and queen number in two boreal *Leptothorax* ants. *Oecologia* 96:32–39.
- Heinze, J., and B. Hölldobler. 1993. Queen polymorphism in an Australian weaver ant, *Polyrhachis cf. doddi*. *Psyche* 100:83–92.
- Janzen, D.H. 1973. Evolution of polygynous obligate Acacia-ants in western Mexico. *J. Anim. Ecol.* 42:727–750.
- Klotz, J. H., B.L. Reid, and W.C. Gordon. 1992. Variation of ommatidia number as a function of worker size in *Camponotus pennsylvanicus* (DeGeer) (Hymenoptera: Formicidae). *Ins. Soc.* 39:233–236.
- Menzel, R., and R. Wehner. 1970. Augenstrukturen bei verschiedengroßen Arbeiterinnen von *Cataglyphis bicolor* Fabr. (Formicidae, Hymenoptera). *Z. vergl. Physiol.* 68:446–449.

- Peeters, C.P. 1991. Ergatoid queens and intercastes in ants: two distinct adult forms which look morphologically intermediate between workers and winged queens. *Ins. Soc.* 38:1–15.
- Pratt, S.C., N.F. Carlin, and P. Calabi. 1994. Division of labor in *Ponera pennsylvanica* (Formicidae: Ponerinae). *Ins. Soc.* 41:43–61.
- Stitz, H. 1939. Hautflügler oder Hymenopteren, I: Ameisen oder Formicidae (Die Tierwelt Deutschlands und der angrenzenden Meeresteile 37). G. Fischer, Jena.
- Taylor, R.W. 1967. A monographic revision of the ant genus *Ponera* Latreille (Hymenoptera: Formicidae). *Pac. Insects Monogr.* 13:1–112.
- Tinaut, A., and J. Heinze. 1992. Wing reduction in ant queens from arid habitats. *Naturwissenschaften* 79:84–85.
- Villet, M.H. 1989. A syndrome leading to ergatoid queens in ponerine ants (Hymenoptera: Formicidae). *J. Nat. Hist.* 23: 825–832.
- \_\_\_\_\_. 1990. Qualitative relations of egg size, egg production and colony size in some Ponerine ants (Hymenoptera: Formicidae). *J. Nat. Hist.* 24:1321–1331.
- Wehner, R., and R. Menzel. 1969. Homing in the ant *Cataglyphis bicolor*. *Science* 164:192–194.