

## KARYOLOGICAL STUDY OF NORTH AMERICAN *POGONOMYRMEX* (HYMENOPTERA : FORMICIDAE) (1, 2)

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### SUMMARY

Karyotypes of 16 taxa of the New World harvester ant genus *Pogonomyrmex* are presented. Species representing both North American subgenera are examined, including members of all four complexes of the nominate subgenus. The nominate subgenus is characterized by a diploid number of 32, whereas *Ephebomyrmex* species have  $2n = 36$  (*P. (E.) huachucanus*) and  $2n = 58-62$  (*P. (E.) imberbiculus*). Chromosome polymorphism was identified only in the latter species.

### RESUME

#### **Etude Caryologique du genre Nord-Américain *Pogonomyrmex* (Hymenoptera : Formicidae)**

Les caryotypes de 16 taxa de la fourmi moissonneuse du genre *Pogonomyrmex* ont été étudiés. Des espèces représentatives des deux sous-genres de l'Amérique du Nord ont été examinées, incluant des membres des quatre complexes du sous-genre *Pogonomyrmex*. Le sous-genre *Pogonomyrmex* est caractérisé par un nombre diploïde de 32, alors que les espèces du sous-genre *Ephebomyrmex* possèdent  $2n = 36$  (*P. (E.) huachucanus*) et  $2n = 58-62$  (*P. (E.) imberbiculus*). Un polymorphisme chromosomique n'a été identifié qu'avec *P. (E.) imberbiculus*.

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## INTRODUCTION

The traditional approach to ant systematics relies entirely upon examination of external morphology with no direct emphasis on genetic characteristics. The size, number, and morphology of the chromosomes are, themselves, useful characters, but their value is enhanced by the fact that chromosomal rearrangements can result in speciation.

Historically, cytotaxonomic studies of Formicidae were initiated when HAUSCHTECK (1961) reported the chromosome numbers of five European species. Subsequent research revealed a general trend toward higher diploid numbers in Formicinae than in Myrmicinae and a correlation of long chromosomes with low numbers. IMAI (1966) reported that ant chromosomes are relatively small and difficult to work with compared to those of many other organisms. After studying 19 Japanese species, IMAI (1966) concluded that (1) myrmicine genera show a wide heteroploid relationship, whereas formicine genera show nearly polyploid relationships; (2) variation in number is wide among related myrmicine species but narrow among formicine species; and (3) in general, chromosome numbers vary greatly within the Formicinae.

Presently, after 20 years of related studies, ca. 500 of the estimated 15,000 living ant species have been karyotyped. These data are useful in the attempt to reconstruct formicid evolution. IMAI *et al.* (1977) proposed three hypotheses for the chromosomal evolution of the ants: (1) the fusion hypothesis—the ancestral species had a high number of chromosomes (ca. 40) with subsequent evolution toward lower numbers; (2) the fission hypothesis—ancestral species had low chromosome numbers and modern species have evolved toward higher numbers; and (3) the modal hypothesis—the present mode is essentially that of the ancestral mode.

Sibling species that are practically indistinguishable on the basis of external morphology may often be recognized by their karyotypes (IMAI *et al.*, 1977). Additionally, morphologically distinct species of some Formicinae reveal identical karyotypes. Identical results were observed among 12 species of the myrmicine genus *Pheidole*. The general rule that karyotypes are rather uniform within species but dissimilar between species does not hold in these cases. However, when cytological investigation reveals significant chromosomal differences between morphologically "identical" species, close examination occasionally discloses visible differences.

Chromosome polymorphism was first detected in a myrmicine ant when populations of the Japanese ant *Pheidole nodus* were identified with haploid chromosome numbers of 17 to 20 (IMAI and KUBOTA, 1972). Every haploid karyotype consisted of 11 submetacentrics or subtelocentrics and two acrocentrics or telocentrics. However, there was considerable variation in the number of metacentrics and telocentrics.

Cytotaxonomic methods were used in the present study toward a much-needed revision of the harvester ant genus *Pogonomyrmex*. This diverse and exclusively New World group is represented by over 60 taxa from southern Canada to Tierra del Fuego. The North American taxa were revised by COLE (1968), but several species have since been described. No similar comprehensive work exists with respect to the Central and South American species.

The status of the subgenus *Ephebomyrmex* is uncertain (TABER *et al.*, 1987). Cytotaxonomic data can help to resolve this problem and may also be useful in the problems presented by many of the taxa within the nominate subgenus. These include the relation of the single North American polymorphic species to its monomorphic congeners, the phylogenetic significance of COLE's (1968) system of complexes, and the status of numerous variants and subspecies within these complexes. Cytological methods allow a fresh approach to these and other problems of harvester ant systematics.

Until now, taxonomic studies of the Myrmicinae genus *Pogonomyrmex* have relied solely upon external morphological characteristics, and many of these are illustrated in a recent scanning electron microscopic study (TABER *et al.*, 1987). The results of a cytotaxonomic study are presented herein. Karyotypes were obtained for all available North American species and compared.

## MATERIALS AND METHODS

Mitotically active cells are required for chromosome preparations, and the early pupal stage of the ant is the best source of material. These were collected directly from the mounds during the summer and fall in Florida, Texas, New Mexico, Arizona, and California. As a consequence of this large sampling effort, an excellent representation of the genus was obtained in terms of subgenera, complexes, and species. Specific collection data, museum and figure numbers for these samples follow in *table 1* (TTU = catalogue number of voucher series in the entomological collection of Texas Tech University).

The method of IMAI *et al.* (1977) was followed with minor modifications. Pharate pupae were selected when available and injected with a 0.01 % aqueous colchicine solution 18 to 24 hours before dissection (COKENDOLPHER and BROWN, 1985). Colchicine prevents the proper formation of spindle fibers during mitosis and results in an accumulation of cells in the metaphase stage. In order to check for any unwanted effects of the drug, colchicine-free larvae were prepared at random intervals during this study. These produced identical results to those of treated larvae, except that fewer metaphase plates were produced. IMAI *et al.* (1977) reported that treated larvae produced chromosomes that were often too highly condensed for C-band analysis.

After 18 to 24 hours of incubation in toweling saturated with 0.01 % aqueous colchicine, the brains of the larvae were removed and placed in a depression slide filled with a hypotonic solution of 1 % aqueous sodium citrate for 20 minutes at room temperature. A single brain was then transferred with a Pasteur pipet to a microscope slide and the excess hypotonic solution was drained off. Several drops of fixative 1 (3:1 glacial acetic acid: absolute ethanol) were applied and drained away. Two additional drops of fixative were then added and after 10 seconds the brain was minced using extremely

Table I. — *Pogonomyrmex* collection data.Tableau I. — Récoltes de *Pogonomyrmex*.

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Subgenus *Pogonomyrmex*
*badius* complex

*Pogonomyrmex badius*. Fig. 1; U.S.A.-Florida: Leon Co., Tallahassee. 25 September 1985, TTU # 6958.

*barbatus* complex

*Pogonomyrmex apache*. Fig. 2; U.S.A.-Arizona: Yavapai Co., Clarksdale. 1 July 1985, TTU # 6831.

*Pogonomyrmex barbatus*. Fig. 3; U.S.A.-Texas: Lubbock Co., Lubbock. 10 June 1985, TTU # 6961.

*Pogonomyrmex desertorum*. Fig. 4; U.S.A.-Arizona: Cochise Co., 4.8 km E Portal. 20 June 1985, TTU # 6754.

*Pogonomyrmex rugosus*. Fig. 5; U.S.A.-California: Los Angeles Co., 28.8 km N Palmdale. 27 June 1985, TTU # 6759.

*maricopa* complex

*Pogonomyrmex californicus*. Fig. 6; U.S.A.-California: Kern Co., Bakersfield. 28 June 1985, TTU # 6778.

*Pogonomyrmex californicus* [*estebanius* sensu Pergande]. Fig. 7; U.S.A.-California: San Bernardino Co., 4.8 km E Apple Valley. 29 June 1985, TTU # 6802.

*Pogonomyrmex comanche*. Fig. 8; U.S.A.-Texas: Houston Co., Grapeland. 24 September 1985, TTU # 6953.

*Pogonomyrmex magnacanthus*. Fig. 9; U.S.A.-California: Riverside Co., 1.6 k W Indio. 30 June 1985, TTU # 6825.

*Pogonomyrmex maricopa*. Fig. 10; U.S.A.-Texas: El Paso Co., 30.4 km E El Paso. 19 June 1985, TTU # 6746.

*occidentalis* complex

*Pogonomyrmex brevispinosus*. Fig. 11; U.S.A.-California: Kern Co., 17.6 km E Shafter. 28 June 1985, TTU # 6782.

*Pogonomyrmex montanus*. Fig. 12; U.S.A. California: San Bernardino Co., 9.6 km E Fawnskin. 29 June 1985, TTU # 6927.

*Pogonomyrmex occidentalis*. Fig. 13; U.S.A.-New Mexico: Grant Co., 24 km E Silver City. 2 July 1985, TTU # 6842.

*Pogonomyrmex subnitidus*. Fig. 14; U.S.A.-California: Los Angeles Co., 8 km S Palmdale. 27 June 1985, TTU # 6763.

Subgenus *Ephebomyrmex*

*Pogonomyrmex huachucanus*. Fig. 15; U.S.A.-Arizona: Cochise Co., Huachuca Mountains, Miller Canyon. 21 June 1985, TTU # 6696.

*Pogonomyrmex imberbiculus*. Fig. 16; U.S.A.-Arizona: Cochise Co., 4.8 km E Portal. 20 June 1985, TTU # 6745. Fig. 17; Texas: Lubbock Co., Lubbock. 10 June 1985, TTU # 6960. TTU # 6959 (same locality and date as 6960) used for additional 2n preparations-no Figs.

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fine teasing needles. Two drops of fixative 2 (1:1 glacial acetic acid: absolute ethanol) were added and after 30 seconds the fluid was drained away. Several drops of fixative 3 (glacial acetic acid) were applied and after 10 seconds the slide was drained again and allowed to dry overnight. The next day the cells were stained for 10 minutes with 1:24 Giemsa Sørensen's buffer (buffer: 4.54 gm  $\text{KH}_2\text{PO}_4$ , 4.75 gm  $\text{Na}_2\text{HP}_4$ , 1,000 ml  $\text{H}_2\text{O}$ ). The taxa studied and the number of replications of this procedure are presented in table II.

The slides were systematically searched for spreads with sets of countable chromosomes and the best of these were photographed. Enlarged prints of each set were prepared and the individual chromosomes were cut out and arranged in numbered, homologous pairs following the system of MACGREGOR and VARLEY (1983). The resulting

Table II. — Analyzed karyotypes from brains of worker ants, ♂ = male, ♀ = female (queen or worker).

Tableau II. — Analyses caryotypiques à partir de cerveaux de fourmis ouvrières, ♂ = mâle, ♀ = femelle (reine ou ouvrière).

Taxon	Chromosome Number (n) 2n	Number of Individuals Observed	Number of Cells Counted	Figure
Subgenus <i>Pogonomyrmex</i>				
<i>badius</i> complex				
<i>P. badius</i>	32	8 ♀	40	1
<i>barbatus</i> complex				
<i>P. apache</i>	32	9 ♀	40	2
<i>P. barbatus</i>	(16) 32	5 ♂, 43 ♀	35, 163	3
<i>P. desertorum</i>	32	5 ♀	19	4
<i>P. rugosus</i>	32	17 ♀	124	5
<i>maricopa</i> complex				
<i>P. californicus</i>	32	13 ♀	59	6
<i>P. californicus</i>	32	4 ♀	10	7
[ <i>estebanius</i> sensu Pergande]				
<i>P. comanche</i>	(16) 32	3 ♂, 9 ♀	24, 61	8
<i>P. magnacanthus</i>	32	5 ♀	89	9
<i>P. maricopa</i>	(16) 32	4 ♂, 15 ♀	22, 68	10
<i>occidentalis</i> complex				
<i>P. brevispinosus</i>	32	2 ♀	7	11
<i>P. montanus</i>	32	6 ♀	14	12
<i>P. occidentalis</i>	32	16 ♀	52	13
<i>P. subnitidus</i>	(16) 32	3 ♂, 23 ♀	13, 88	14
Subgenus <i>Ephebomyrmex</i>				
<i>P. huachucanus</i>	36	12 ♀	89	15
<i>P. imberbicus</i>	(30) 58-62	1 ♂, 14 ♀	30 = 1, 58 = 18, 59 = 10, 60 = 6, 61 = 101, 62 = 73	16, 17

karyotypes of each species were then analyzed and compared. We have used the term "metacentric" in a broad sense which includes submetacentric chromosomes. Likewise, "acrocentric" includes chromosomes with subtelocentric centromeres. Those chromosomes which have visible centromeres have been identified accordingly.

## RESULTS AND DISCUSSION

The biological material of the karyotypic study included 217 individuals from 69 colonies and this resulted in a total of 1,225 countable chromosome sets. The data that can be extracted from these karyotypes include the diploid (or haploid) number of the cell and the size and centromere position of individual chromosomes. As previously noted, the chromosomes of ants tend to be relatively small and this sometimes makes both the identification of homologous pairs and the centromere position difficult to determine. The diploid numbers obtained for each available species are presented in *table II*.

### KARYOTYPES OF *POGONOMYRMEX*

#### **Subgenus *Pogonomyrmex***

Species of the nominate subgenus have diploid numbers of 32. The karyotypes are composed of predominantly metacentric and submetacentric chromosomes, and the frequency of acrocentric and subtelocentric chromosomes is apparently highest within the *occidentalis* complex.

#### **The *badius* complex**

*Pogonomyrmex badius* is the only member of this complex. Chromosome pairs 1-10, 12, and 14 are metacentric (*fig. 1*).

#### **The *barbatus* complex**

Distinct banding patterns are visible in the primarily metacentric chromosomes of *P. apache* (*fig. 2*). Chromosomes 1-9 of a haploid male *P. barbatus* ( $n = 16$ ) are metacentric (*fig. 3*). Chromosome pairs 1-7 and 11-13 in the karyotype of *P. desertorum* are also metacentric (*fig. 4*). A karyotype of *P. rugosus* reveals moniliform chromosomes (*fig. 5*). Except for those of pairs 3, 4, and 16, the centromere positions are visible and the chromosomes are metacentric.

#### **The *maricopa* complex**

Chromosome pairs 1-10 of *P. californicus* are metacentric (*fig. 6*). The chromosomes of *P. californicus* [*estebanius* sensu Pergande] are also primarily metacentric, but pairs 10 and 15 might be acrocentric (*fig. 7*). The

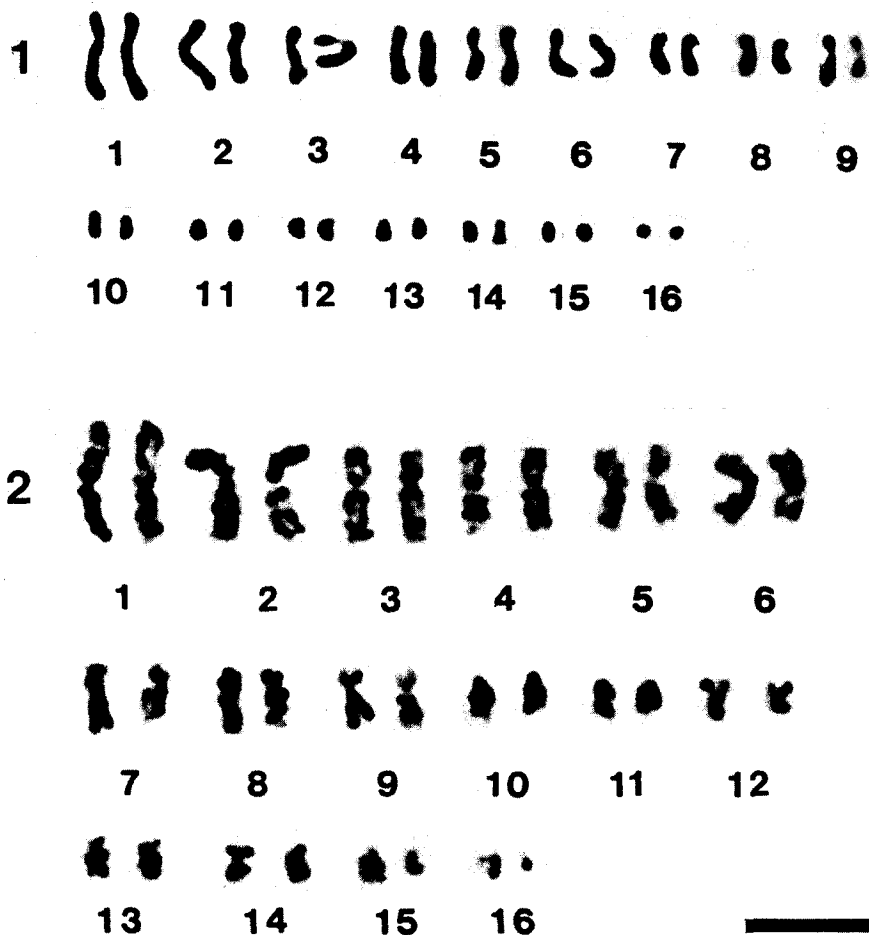


Fig. 1 and 2. — *Pogonomyrmex* karyotypes: 1, *P. badius* ♀. 2, *P. apache* ♀. Scale line = 5  $\mu$ m.

Fig. 1 et 2. — Caryotypes de *Pogonomyrmex*: 1, *P. badius* ♀. 2, *P. apache* ♀. Echelle = 5  $\mu$ m.

two smallest pairs also appear to be acrocentric. This subspecies was synonymized under *P. californicus* by COLE (1968). The subspecific name was given to those taxa which are bicolored (the gaster is brown or black and the anterior portion of the ant is red). COLE (1968) and TABER *et al.* (1987) reported that the bicolored form also differed in the amount and size of cephalic and pronotal rugae. The karyotypes of *estebanius* and *californicus* proper differ slightly in centromere positions, but further samples, including those from intermediate populations, are needed before the status of the

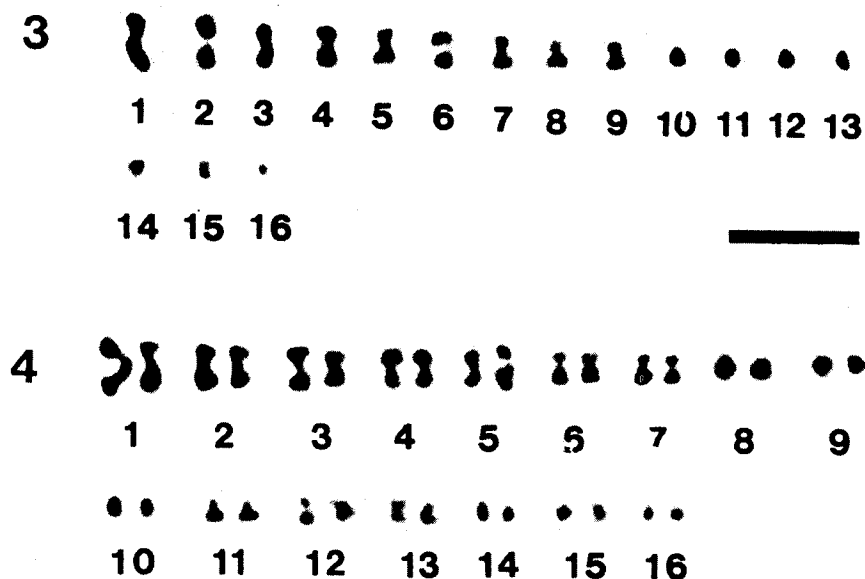


Fig. 3 and 4. — *Pogonomyrmex* karyotypes: 3, *P. barbatus* ♂. 4, *P. desertorum* ♀. Scale line = 5  $\mu$ m.

Fig. 3 et 4. — Caryotypes de *Pogonomyrmex*: 3, *P. barbatus* ♂. 4, *P. desertorum* ♀. Echelle = 5  $\mu$ m.

bicolored population can be accurately determined. KNUDTSON (1978) found no significant electrophoretic differences between the two color morphs. *Pogonomyrmex comanche* was originally described as a subspecies of *P. occidentalis*, a member of another species complex, by WHEELER (1902), who also noted its morphological similarity to *P. subnitidus*. Pairs 1-9 of the karyotype of *P. comanche* are metacentric but the centromere positions of the remaining pairs are not clearly visible (fig. 8). Although COLE (1968) placed this species in the *maricopa* complex, its karyotype is similar in appearance to those of *P. occidentalis* and *P. subnitidus*. Only one colony of *P. magnacanthus* was examined and its karyotype reveals metacentrics in pairs 1-10, 13, and 15 (fig. 9). The haploid karyotype of a male *P. maricopa* reveals metacentric chromosomes 1-9 (fig. 10) and chromosome 10 is either submetacentric or subtelocentric.

#### The *occidentalis* complex

Only one colony of *P. brevispinosus* was collected. The first 10 pairs of chromosomes are metacentric, as is pair 15 (fig. 11). Pairs 1-10 and pair 15





Fig. 5 and 6. — *Pogonomyrmex* karyotypes: 5, *P. rugosus* ♀. 6, *P. californicus* ♀. Scale line = 5  $\mu$ m.

Fig. 5 et 6 — Caryotypes de *Pogonomyrmex*: 5, *P. rugosus* ♀. 6, *P. californicus* ♀. Echelle = 5  $\mu$ m.

of the *P. montanus* karyotype are also metacentric (fig. 12). *Pogonomyrmex occidentalis* has metacentric chromosomes in pairs 1-9 and pair 13, but pairs 10-12, 14, and 15 are acrocentric (fig. 13). MEHLHOP and GARDNER (1982) also obtained  $2n = 32$  for *P. occidentalis*. The karyotype of *P. subnitidus* reveals metacentrics in pairs 1-10, 13, 14, and 16. The remaining pairs are composed of acrocentrics (fig. 14).

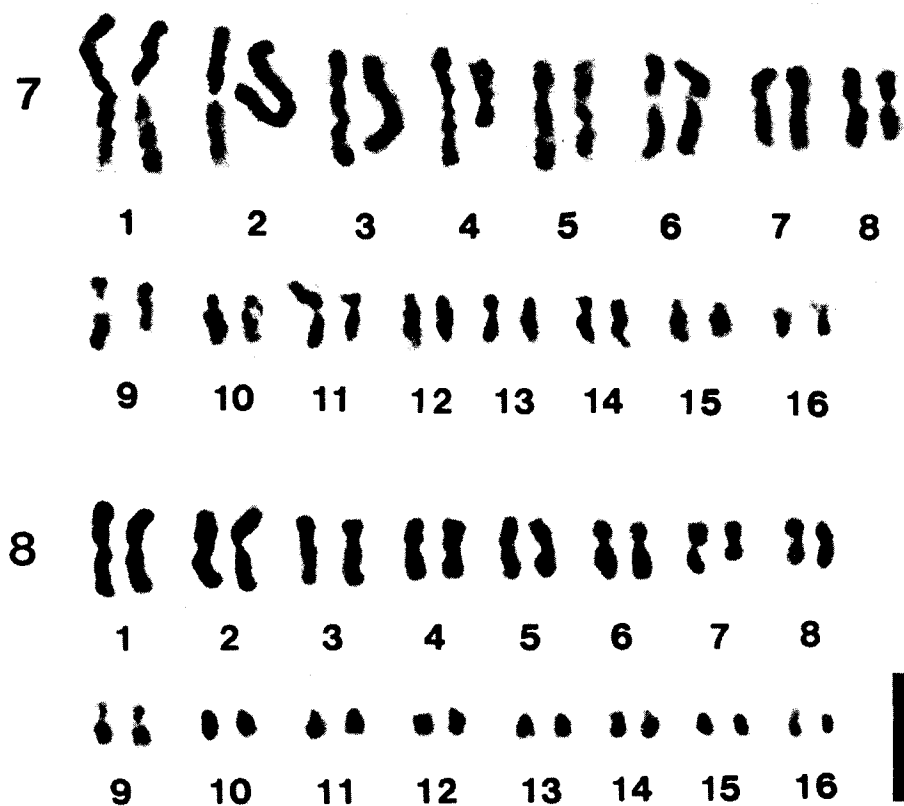


Fig. 7 and 8. — *Pogonomyrmex* karyotypes: 7, *P. californicus* [*estebanius* sensu Pergande] ♀. 8, *P. comanche* ♀. Scale line = 5  $\mu$ m.

Fig. 7 et 8. — Caryotypes de *Pogonomyrmex*: 7, *P. californicus* [*estebanius* sensu Pergande] ♀. 8, *P. comanche* ♀. Echelle = 5  $\mu$ m.

### Subgenus *Ephebomyrmex*

One colony of *P. huachucanus* was sampled and the karyotypes of these specimens contain 36 chromosomes (fig. 15). Pairs 1-3, 5, 7, and 15-18 are composed of metacentrics. Pairs 4, 6, 11, and 13 appear to be acrocentric. There are 30 chromosomes in the haploid karyotype of a male *P. imberbiculus* (fig. 16). Chromosomes 1-10 are acrocentrics and chromosomes 11-18, 21, 28, and 29 are metacentrics. A diploid spread from a worker has  $2n = 61$  (fig. 17). Pairs 1-15 are submetacentrics and subtelocentrics and pairs 16-19, 21, 23, and 25-27 are metacentrics in the broad sense. One chromosome lacks a homolog. There were 208 karyotypes available for analysis and the variation in number ranged from 58 to 62 chromosomes. Different indi-

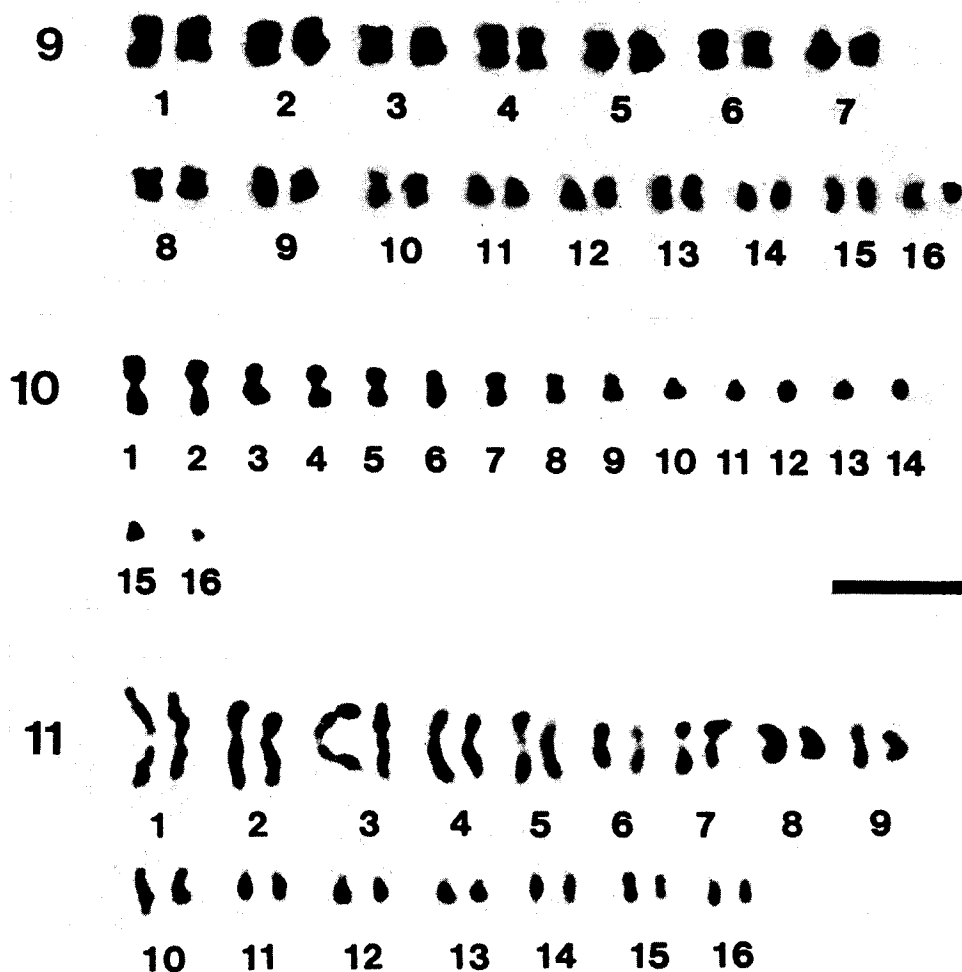


Fig. 9, 10 and 11. — *Pogonomyrmex* karyotypes: 9, *P. magnacanthus* ♀. 10, *P. maricopa* ♂. 11, *P. brevispinosus* ♀. Scale line = 5  $\mu$ m.

Fig. 9, 10 et 11. — Caryotypes de *Pogonomyrmex*: 9, *P. magnacanthus* ♀. 10, *P. maricopa* ♂. 11, *P. brevispinosus* ♀. Echelle = 5  $\mu$ m.

viduals from one colony (TTU  $\pm$  6959) revealed diploid numbers of 60, 61, and 62. Two ants from the colony of figure 17 (TTU  $\pm$  6960) possessed 58 chromosomes per cell. Counts were obtained from 12 cells in one individual and from six in the other. A third individual possessed a diploid number of 60 (six cells). These differences in chromosome number might be due to super-numerary chromosomes (CROZIER, 1977).

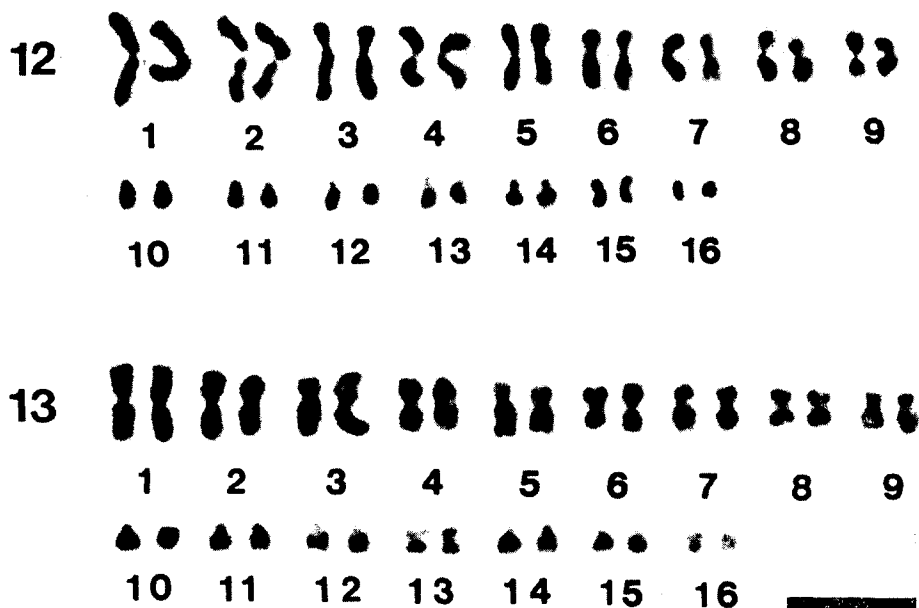


Fig. 12 and 13. — *Pogonomyrmex* karyotypes: 12, *P. montanus* ♀. 13, *P. occidentalis* ♀. Scale line = 5  $\mu$ m.

Fig. 12 et 13. — Caryotypes de *Pogonomyrmex*: 12, *P. montanus* ♀. 13, *P. occidentalis* ♀. Echelle = 5  $\mu$ m.

The chromosomes of 16 North American taxa of *Pogonomyrmex* have been reported upon herein, but a complete phylogenetic reconstruction of the genus requires additional data. The karyotypes of the remaining North American taxa and those of approximately 40 Central and South American species are needed to help achieve this goal.

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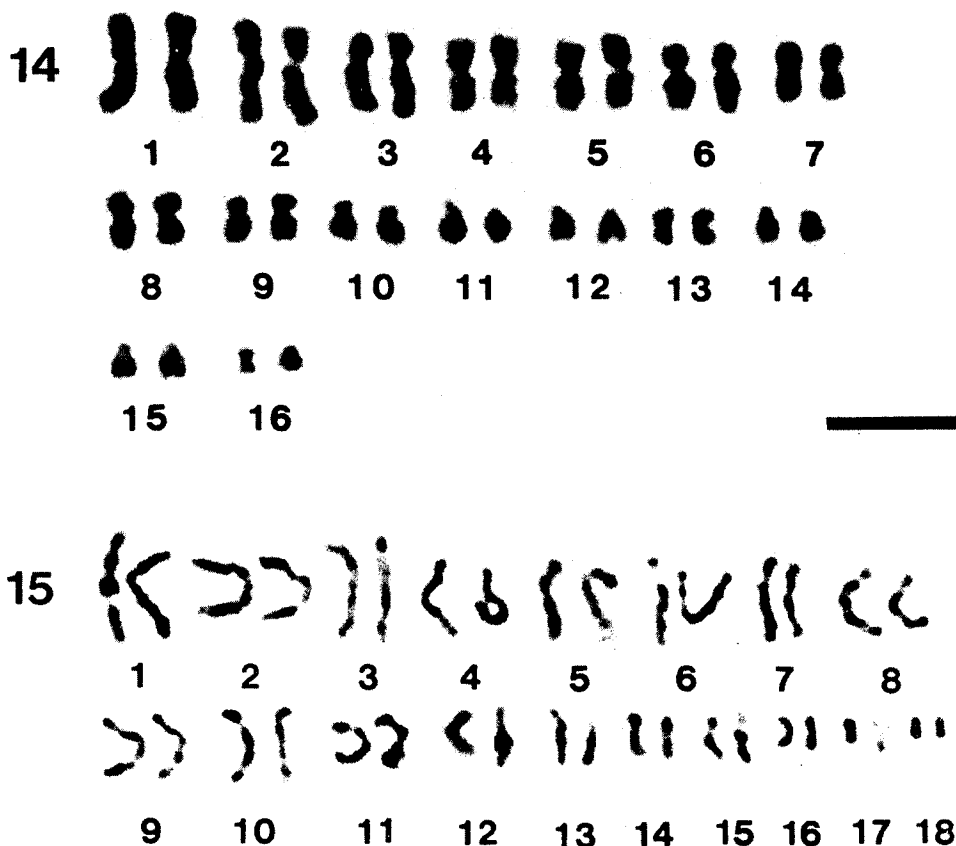


Fig. 14 and 15. — *Pogonomyrmex* karyotypes : 14, *P. subnitidus* ♀. 15, *P. huachucanus* ♀. Scale line = 5  $\mu$ m.

Fig. 14 et 15. — Caryotypes de *Pogonomyrmex* : 14, *P. subnitidus* ♀. 15, *P. huachucanus* ♀. Echelle = 5  $\mu$ m.

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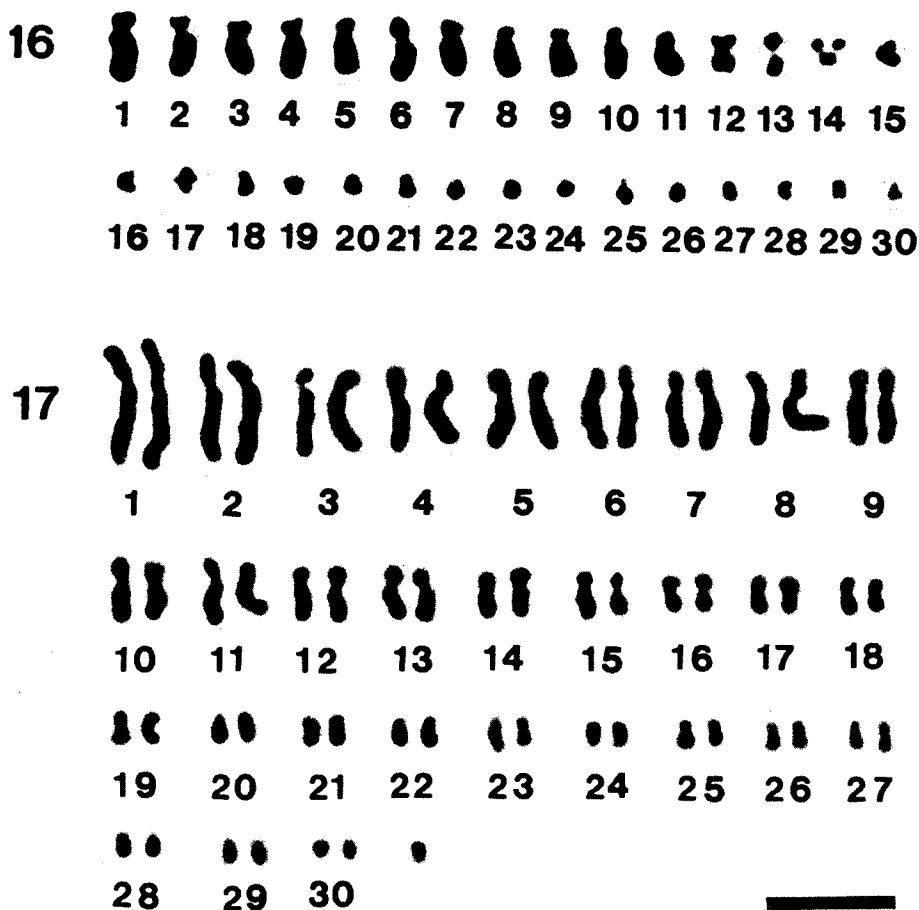


Fig. 16 and 17. — *Pogonomyrmex* karyotypes: 16, *P. imberbiculus* ♂. 17, *P. imberbiculus* ♀. Scale line = 5  $\mu$ m.

Fig. 16 et 17. — Caryotypes de *Pogonomyrmex*: 16, *P. imberbiculus* ♂. 17, *P. imberbiculus* ♀. Echelle = 5  $\mu$ m.

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