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KARYOTYPES OF TWENTY-ONE ANT SPECIES (HYMENOPTERA; FORMICIDAE), WITH REVIEWS OF THE KNOWN ANT KARYOTYPES

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Six dolichoderine species have haploid numbers: 9 (*Iridomyrmex pilifer*, *I.* sp. nr. *pilifer*, *Dorymyrmex ?thoracicus*, *D. ?pulchellus*), 13 (*D. bicolor*) and 16 (*Forelius foetidus*). Robertsonian changes could account for the differences between the *Dorymyrmex* numbers. The *Iridomyrmex* species, both Neotropical, have a different karyotype from Australian 9-chromosome *Iridomyrmex*. The species with numbers 13 and 16 have relatively more acrocentrics per karyotype than those with lower numbers. Five formicine species have haploid numbers: 8 (*Oecophylla smaragdina*), 9 (*Brachymyrmex* sp.), 15 (*Lasius nearcticus*), 21 (*Polyrhachis rastellata*), and 26 (*Camponotus* (*Colobopsis*) sp. (*impressus* gp.)). Although thelytoky has been reported for *Oecophylla* spp., a queenless greenhouse colony died out after producing an all-male brood; further work is suggested on *Oecophylla* populations where thelytoky has been reported. The 8- and 9-chromosome formicines have all chromosomes metacentric, while acrocentrics predominate in the higher-numbered species. The ponerine *Proceratium silaceum* has $n = 18$. Nine myrmicine species have haploid numbers: 10 (*Pheidole dentata*, *P. dentigula*), 11 *Solenopsis molesta*, *Monomorium minimum*, *M. viridum*, *Meranoplus* sp. (*hirsutus* gp.)), 12 (*Leptothorax longispinosus*), and 16 (*Solenopsis aurea*, *S. geminata*). *Monomorium* karyotypes have a small acrocentric, while all 11-chromosome *Solenopsis* chromosomes are metacentric. Reviewing the 92 known ant karyotypes supports some present taxonomic schemes but not others. Imai's (1966) suggestions, that polyploidy occurred in formicine evolution and that high numbers occur more frequently at 'high' latitudes, are not supported by present evidence.

Introduction

Although ants were among the first Hymenoptera studied (Henking, 1892; Schleip, 1908; Lams, 1908; Hogben, 1920), interest in them as cytological material then lagged behind that in other Hymenoptera until the last two decades. Most work on Hymenoptera until very recently was carried out on sawflies and parasitic forms. This lapse in interest in ant chromosomes was undoubtedly caused by the earlier workers choosing ant species that happened to have high chromosome numbers or exhibited other features likely to cause technical difficulties, rather than to intrinsic disadvantages to the study of ant chromosomes in general; in fact, ants have proven more suitable for cytological studies than most other Hymenoptera.

The first 'modern' papers on ant cytogenetics were those of Whelden and Haskins (1953) and Ledoux (1954). Both of these papers contain serious flaws, and it is Smith and Peacock's (1957) paper on *Monomorium pharaonis* that stands as the first reliable paper on ant cytogenetics. This paper, part of Peacock's comprehensive study of the biology of *M. pharaonis*, remains the best general account of the cytology of gametogenesis in an ant, although techniques for elucidating chromosome morphology have improved markedly since.

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The survey period of ant cytogenetics was launched by Hauschteck (1961, 1962, 1963, 1965), working chiefly on European species. Imai (Imai and Yosida, 1964, 1965a,b; Imai, 1966) and Crozier (1968a,b,c, 1969a,b) have extended this survey to Japanese, Australian and New World species. Other recent papers have been those of Kumbkarni (1965) and Hung (1969).

Smith and Peacock's (1957) figures enable determination of centromere position for the chromosomes of *Monomorium pharaonis* but, until my own and papers by Imai appeared, general information on centromere position in ant chromosomes was not forthcoming. Imai's (1966) figures show centromere positions well in many cases, but unfortunately he does not discuss this point in his text. The determination of centromere positions in ant karyotypes should become standard once the use of air-drying techniques spreads (e.g., Crozier, 1968a).

Metacentric chromosomes predominate in most ant karyotypes, exceptions being *Rhytidoponera* karyotypes (excluding the $n = 12$ population (Crozier (1969b)), and those of *Lasius nearcticus*, *Forelius foetidus*, *Dorymyrmex bicolor*, *Camponotus* (*Colobopsis*) sp., *Polyrhachis* sp. (this report) some New World *Aphaenogaster* taxa (Crozier, unpublished), and possibly the *Formica* species worked on by Imai. The importance of determining centromere position is shown by the discovery of polymorphisms for centromere position in some species, probably indicating inversion polymorphisms.

In reviewing the karyotypes found in each ant subfamily, I have generally cited only one paper, the most comprehensive or most recent, in the case of authors who have worked on a given species more than once. I have also omitted work of doubtful validity, including the four early papers, whose chromosome counts have not been confirmed by later workers (Schleip found $n = 24$ for *Formica sanguinea* as against $n = 26$ found by Imai and Yosida (1964) and Hogben (1920) found *Lasius flavus* to have $n = 11$ whereas Hauschteck (1962) reports it to have $n = 15$).

Methods

Air-drying Technique of Chromosome Preparation

The squash technique proved inadequate for routine analysis of many individuals, and so an air-drying technique was developed. The technique developed (Crozier, 1968a) has been found suitable for use with *Drosophila* and ants; a strikingly similar technique has since been developed (Meredith, 1969) for use with mammalian testes. The treatment schedule for ants, slightly modified from the previously published form, is as below:

(1) Puncture live prepupae or early male pupae with a minuten pin and place them in a small watchglass containing some colcemid-Ringer solution (0.05% colcemid (Ciba) in insect Ringer: NaCl, 14.0 gm/liter; $CaCl_2$, 0.4 gm/liter; KCl, 0.2 gm/liter; $NaHCO_3$, 0.2 gm/liter); turn the organism over to place the puncture below the liquid surface. Cover and leave at 20 to 25° C (room temperature) for about 15 hours.

(2) Dissect out the desired organs (cerebral ganglia, testes) under 1% sodium citrate and transfer them to fresh citrate, using scoops made out of plastic capillary tubing. Leave them in citrate for 10 to 20 minutes.

(3) Transfer organs to acetic-methanol (1:3) fixative for 30 minutes.

(4) Transfer to drop of 60% acetic acid (aqueous) on a clean warmed slide. If the tissue does not rapidly dissociate, macerate using bent minuten pins.

(5) Rapidly encircle the 60% acetic acid cell suspension with acetic-methanol fixative and add a drop of the fixative to the cell suspension drop. Using a rubber bulb such as an ear syringe, disperse the cell suspension over the slide and maintain an air flow until the slide is dry.

(6) Place the slides in acetic-ethanol (1:3) fixative for 2 hours, to reduce cytoplasmic staining.

(7) Rinse the slides in the stain solvent, to reduce subsequent stain precipitation.

(8) Stain the preparations using a solution consisting of: orcein, 1 gm; 85% lactic acid, 28 ml; glacial acetic acid, 22 ml (after Imai, 1966). Place rectangular slivers of coverslip at either end of the area to be stained, to support a coverslip. After applying some four drops of stain, cover the preparation with a coverslip (24 × 50 mm) to spread the stain, and place in a covered container (e.g., a 6″ cheese dish) on a hot plate set at about 50° C. Leave for 2 to 3 hours, after which the slides can be removed from the hot plate and left at room temperature until the next day.

(9) Place slides vertically in 70% ethanol and allow the coverslips to slide off.

(10) Dehydrate with 95% ethanol and two changes of absolute ethanol and mount in Euparal.

Examination of Preparations

Determination of the chromosome number of an individual: In most cases, 20 'good' cells, of the same ploidy level as could be seen in the majority of cells during cursory examination, were examined for each slide and the number of chromosomes in each counted using a hand counter. If fewer than half of these had the same number, or if any cell was found which had a higher number than this most common number, then an additional number of cells, at least 10, was examined. This quota was usually achieved quickly or not at all; many more cells were then examined in a search for cells to photograph. Conclusions based on the counts of 20 cells were always in agreement with what was seen upon further examination. Cells seen with lower numbers than the number of the individual were clearly due to cell fragmentation. As well as a few cells at higher levels of ploidy, occasional cells were encountered with one or two chromosomes more than the number determined for that individual; these anomalous results could often be seen to be due to such causes as chromosome breakage or the persistence of fragments of other cells (detected through differences in condensation of the additional chromosomes), and I believe that all such cases are due to these or similar causes.

Determination of haploid number: In organisms with no sexual differentiation of karyotype except for degree of ploidy, determination of a number as haploid or diploid presents a problem not encountered in species with both sexes diploid. Where both haploid and diploid individuals were encountered, the problem was readily resolved. Otherwise, careful attention had to be paid to details of morphology in prepupae that serve to distinguish the sexes (pupae are readily sexed, having the adult form, but are less suitable as cytological material). These characters are the presence or absence of testes, and the morphology of the antennae – males usually have long antennae with segments of approximately equal length, while females have the first antennal segments about as long as the rest combined, the antennae thus being 'elbowed'.

Chromosome classification: Levan *et al.* (1964) have proposed a standard nomenclature for centromere position that I follow here, save that chromosomes termed subtelocentric under their system will here be termed subacrocentric and the term acrocentric will be used to refer to all chromosomes with an arm ratio greater than 7.0. The arm ratio, r, is the ratio of the length of the long arm of a chromosome to that of the short arm. Metacentric chromosomes are those with $r = 1.0 - 1.7$, submetacentrics have $r = 1.7 - 3.0$, subacrocentrics have $r = 3.0 - 7.0$ and acrocentrics have values of 7.0 and above. In many cases, of course, especially where small chromosomes are involved, it is not possible to classify chromosomes as other than metacentric-to-submetacentric or subacrocentric-to-acrocentric. Classification is by visual comparison of photographed chromosomes with drawings of the different types, based on figures given by Levan *et al.* (1964).

Number of individuals examined per colony: If all ant species were invariant with respect to karyotype, examination of one preparation per species would suffice. Since this is not so, however, sufficient individuals should be examined per colony to enable detection of any variation. Many species have polygynous (multiple-queen) colonies, and in the absence of additional data it is uncertain how many individuals should be examined in these cases. However, for the simple case where there is only one queen per colony, and she has been inseminated once, the chances of detecting intra-colony karyotype variation through examination of her progeny is given by:

$$P = 1 - p^n - q^n$$

where P = probability of the sample containing both types of gametes
n = number of individuals in sample
$p = q = 0.5$ = frequencies of the two types of gametes assuming normal behavior at meiosis.

therefore,

$$P = 1 - (0.5)^{n-1}$$

As seen from the above equation, there is a 93.75% chance of detecting heterozygosity of the queen through examination of a sample of five individuals, and one of 96.87% for a sample of six. Accordingly, six has been taken as the number to be aimed at in deciding how many preparations to make and examine, a goal not always achieved. Note that the equation applies to worker samples as well as to males, because the paternal contributions, being identical, add nothing to any sample heterogeneity. Examination of males only yields information on the queen's genotype; whereas examination of workers also yields information on the genotype of the male that inseminated the queen. Worker-laid eggs, however, are a possible source of contamination, making reliance on any ratios obtained unwise.

Identification and Deposition of Voucher Specimens

Adult voucher specimens were determined either by Dr. W. L. Brown, Jr., or the author. Australian specimens will be deposited in the Australian National Insect Collection, held by the Division of Entomology, C.S.I.R.O., Canberra, A.C.T., Australia; all other specimens will be deposited in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.

All voucher specimens bear colony collection numbers (e.g., AABD. 1), which correspond to numbers given on each slide.

Observations

Subfamily Dolichoderinae

Karyotypes of Six Species

Iridomyrmex pilifer: $n = 9$, Fig. 1A. One colony, two diploids, examined; taken at Macchu Pichu, Peru.

Seven large metacentrics, two small acrocentrics. The acrocentrics are usually present as four small dots in diploid metaphases. A larger pair with a slightly higher arm ratio than the rest can sometimes be distinguished among the metacentric chromosomes.

Iridomyrmex sp. nr. *pilifer*: $n = 9$, Fig. 1B. On colony, three diploids; taken at Tingo Maria, Peru.

This karyotype cannot be distinguished from that of *I. pilifer*. Although few individuals of each were examined, the similarity of the karyotypes of this species and *I. pilifer* suggests that the observed karyotype is probably representative of both species.

Forelius foetidus: $n = 16$, Fig. 1C. Three colonies: two diploids from one taken near Cortaro, Arizona, U.S.A., four haploids and one diploid from

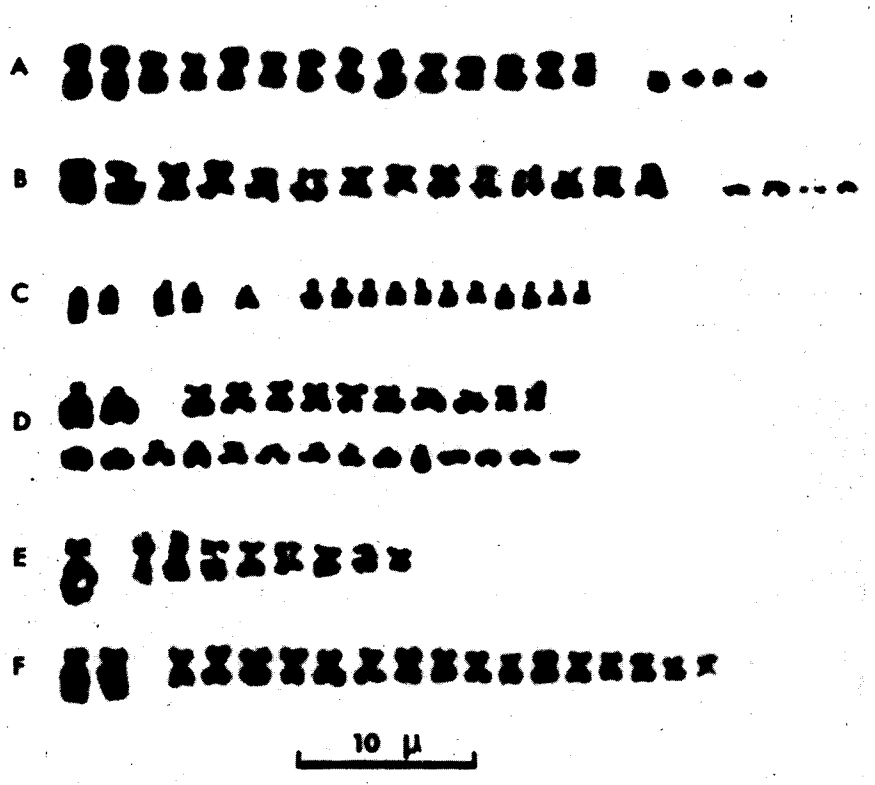

Fig. 1. The karyotypes of six species of Dolichoderinae. A. *Iridomyrmex pilifer*, $2n = 18$. B. *Iridomyrmex* sp. nr. *pilifer*, $2n = 18$. C. *Forelius foetidus*, $n = 16$. D. *Dorymyrmex bicolor*, $2n = 26$. E. *D. ?thoracicus*, $n = 9$. F. *D. ?pulchellus*, $2n = 18$.

one taken in Sabino Canyon, Santa Catalina Mountains, Arizona and two haploids from one taken near Tucson, Arizona.

The chromosomes of this species proved difficult to elucidate, due to their small size and the tendency of the acrocentrics and subacrocentrics to become contorted into 'w' and rectangular configurations. One good cell is shown; other cells are generally consistent with it, but it is possible that some undetected variation occurs. Four groups can be distinguished:

A chromosomes 1 and 2	large, acrocentric
B chromosomes 3 and 4	large, subacrocentric
C chromosome 5	medium, acrocentric
D chromosomes 6 – 16	medium, submetacentic to subacrocentric.

Dorymyrmex bicolor: $n = 13$, Fig. 1D. Two colonies, seven diploids from one, one diploid from the other; both taken from a sandy wash near Cortaro, Arizona, U.S.A.

One large acrocentric-to-subacrocentric, five medium-sized metacentrics, seven acrocentrics-to-submetacentrics ranging in size from medium to small.

Dorymyrmex ?thoracicus: $n = 9$, Fig. 1E. One colony, one haploid; taken near La Molina, near Lima, Peru.

One large and eight medium-sized metacentrics. Since only one specimen has been examined, nothing can be said about karyotype variation in this species, but the differences between this karyotype and that of *D. bicolor* are very striking in view of the fact that the workers of the two species cannot be distinguished using external morphology.

Dorymyrmex ?pulchellus: $n = 9$, Fig. 1F. One colony, four diploids; taken at the Cidade Universitaria, São Paulo, Brasil.

This karyotype, first figured in Crozier (1968a), is essentially the same as that of *D. ?thoracicus*, with one large submetacentric, almost subacrocentric, chromosome and eight medium-sized metacentric chromosomes. Whereas the workers of *D. ?thoracicus*, like those of *D. bicolor*, are bicolored red and black, those of *D. pulchellus* are uniformly very dark brown to black.

Subfamily Formicinae

Karyotypes of Five Species

Brachymyrmex sp.: $n = 9$, Fig. 2A. One polygynous colony, five diploids; taken at Horto Florestal, Serra do Cantareira, São Paulo, Brasil.

All chromosomes metacentric, with a continuous range of size.

Lasius nearcticus: $n = 15$, Fig. 2B. One colony, six diploids; taken on the Cornell Campus, Tompkins County, New York State, U.S.A.

One metacentric and 14 acrocentrics. The metacentric is smaller than the largest acrocentric. The acrocentric chromosomes range continuously in size.

Camponotus (*Colobopsis*) sp. (*impressus* group): $n = 26$, Fig. 2C. Two colonies, four diploids in one, three haploids and two diploids in the other; both colonies taken at Austin, Texas, U.S.A.

The chromosomes of this species are nearly all acrocentric or subacrocentric, with possibly some submetacentrics amongst the smallest members, most of which cannot be seen clearly. Although there is a great range of size, from medium to very small, there are no sharp breaks and hence no discernible groups.

Polyrhachis rastellata: $n = 21$, Fig. 2D. One colony, three haploids; the nest consisted of a leaf fastened by carton to a palm frond, and was found at Frazer's Hill, Selangor, Malaysia.

Four metacentrics and 17 subacrocentric to acrocentric chromosomes.

Oecophylla smaragdina: $n = 8$, Fig. 2E. One colony, six haploids and one diploid; taken in the grounds of the Faculty of Agriculture, University of Malaya, Kuala Lumpur, Malaysia. Eight metacentrics, varying in size but without discernible groups. The largest chromosome is sometimes almost submetacentric, but more often has arms of very nearly equal length. An achromatic gap, or secondary constriction, is sometimes present on one of the larger chromosomes (e.g., the third in Fig. 2E).

Biological Note on Oecophylla smaragdina

A number of leaf-nests of the original colony were cut from the host tree and transported to Ithaca, where the ants were kept in a small greenhouse under simulated rainforest conditions. No queen was seen among the ants; she probably remained in one of the nests too high to reach on the original tree. Although there had been significant mortality during the transport of the ants to Ithaca, the survivors appeared vigorous upon transfer to the greenhouse. While in Ithaca, the ants were very active. They made a number of nests, and egg production was apparently high, followed by the appearance of many larvae. Except for one worker pupa found within one month of the establishment of the colony fragment in the greenhouse, all adults produced in Ithaca were males. The colony persisted for about 11 months, with fewer and fewer workers and increasing numbers of males, before declining and disappearing.

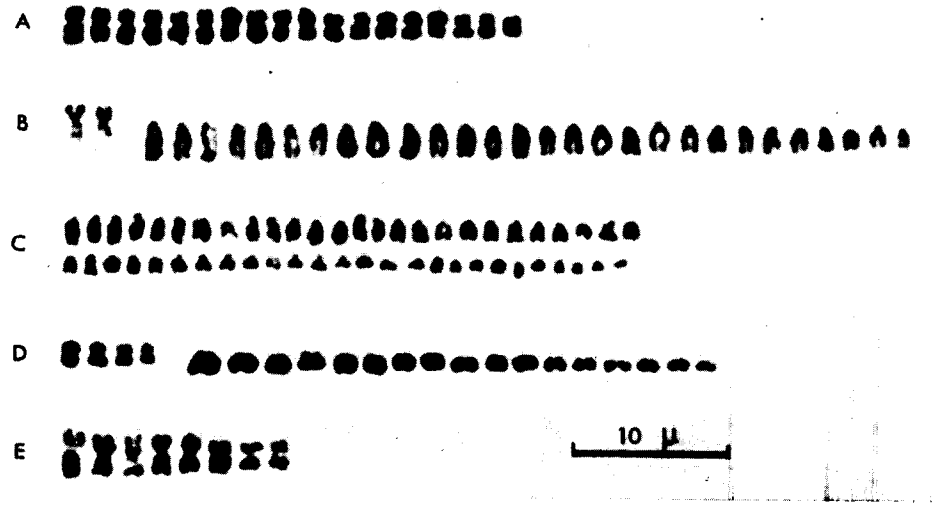

Fig. 2. Karyotypes of five formicine species. A. *Brachymyrmex* sp., $2n = 18$. B. *Lasius nearcticus*, $2n = 30$. C. *Camponotus* (*Colobopsis*) sp. (*impressus* gp.), $2n = 52$. D. *Polyrhachis rastellata*, $n = 21$. E. *Oecophylla smaragdina*, $n = 8$.

Subfamily Ponerinae

Proceratium silaceum: $n = 18$, Fig. 3A. One colony, three haploids and three diploids; taken at Shoal Creek Camp Ground, Jackson County, North Carolina, U.S.A.

One large submetacentric, one large subacrocentric, and 16 metacentric to submetacentric chromosomes. A larger metacentric to submetacentric can sometimes be distinguished among the third group chromosomes, but I could not determine whether this is a genetic variant or due to inequalities of air-drying of the cells involved.

Subfamily Myrmicinae

Karyotypes of Nine Species

Solenopsis aurea: $n = 16$, Fig. 4A. One colony, four diploids; taken at College Peak, Cochise County, Arizona, U.S.A.

Sixteen large to medium-sized metacentric to submetacentric chromosomes. Although there is some variation between chromosomes in size and centromere position, there are no clearly discernible groups.

Solenopsis geminata: $n = 16$, Fig. 4B. Two colonies, six diploids in one and one diploid in the other; supplied by Dr. E. O. Wilson, Harvard University, from laboratory colonies believed to have originated in Alabama, U.S.A.

Seven large to medium metacentrics and nine large to medium subacrocentrics. One of the metacentrics is sometimes distinguishable from the rest as being smaller and having a slightly higher arm ratio than the rest.

Solenopsis molesta: $n = 11$, Fig. 4C. One colony, six diploids; taken at South Lansing, Tompkins County, New York State, U.S.A.

All chromosomes medium-sized metacentrics. There is little size variation, although the largest chromosome does stand out a little from the rest.

Monomorium minimum: $n = 11$, Fig. 4D. One polygynous colony, five diploids; taken at Bennett State Park, Jackson County, Texas, U.S.A.

One large submetacentric to subacrocentric chromosome, nine large to medium metacentrics, and one small subacrocentric to acrocentric chromosome.

Monomorium viridum: $n = 11$, Fig. 4E. One polygynous colony, six diploids; taken at Lebanon State Forest, New Jersey, U.S.A.

One large submetacentric to subacrocentric chromosome, nine large to medium metacentrics, and one small acrocentric chromosome. This karyotype

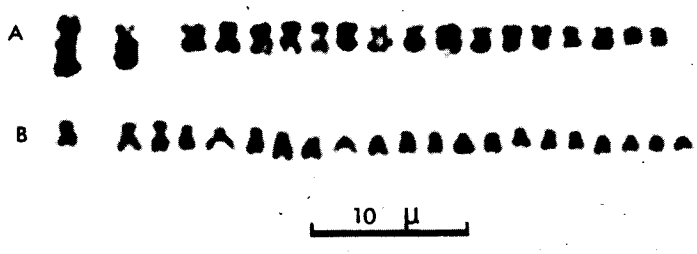

Fig. 3. Karyotype of *Proceratium silaceum* compared with that of another ponerine. A. *P. silaceum*, $n = 18$. B. *Rhytidoponera victoriae*, $n = 21$.

appears the same as that of *M. minimum*, except that the smallest chromosome in *M. viridum* karyotypes is always strictly acrocentric in appearance, whereas a short arm can often be seen on the corresponding chromosome in *M. minimum* karyotypes.

Pheidole dentata: $n = 10$, Fig. 5A, B. Two colonies, six diploids each; taken at O'Leno State Park, Florida, U.S.A., and at Buescher State Park, Bastrop County, Texas, U.S.A.

The Florida colony workers were black, the Texas colony workers dark brown. The Florida karyotype comprises 10 large to medium-sized submetacentrics and metacentrics. The three largest are submetacentric, two of these almost subacrocentric in some cells. The rest of the chromosomes are metacentric. The Texas karyotype appears to be the same, except that I am not sure that the third largest chromosome is submetacentric here also.

Pheidole dentigula: $n = 10$, Fig. 5C. One colony, six diploids; Alexander Springs, Florida, U.S.A.

Ten medium-sized submetacentrics and metacentrics. The two largest chromosomes are submetacentric; the rest, metacentric.

Leptothorax longispinosus: $n = 12$, Fig. 5D. One colony, three haploids and three diploids; taken at Stewart Park, Tompkins County, New York, U.S.A.

Eleven large submetacentrics and metacentrics and one subacrocentric to acrocentric chromosome.

Meranoplus sp. (*hirsutus* group): $n = 11$, Fig. 5E. One colony, three diploids; taken in rain forest on the Black Mountain Road, near Kuranda, Queensland, Australia.

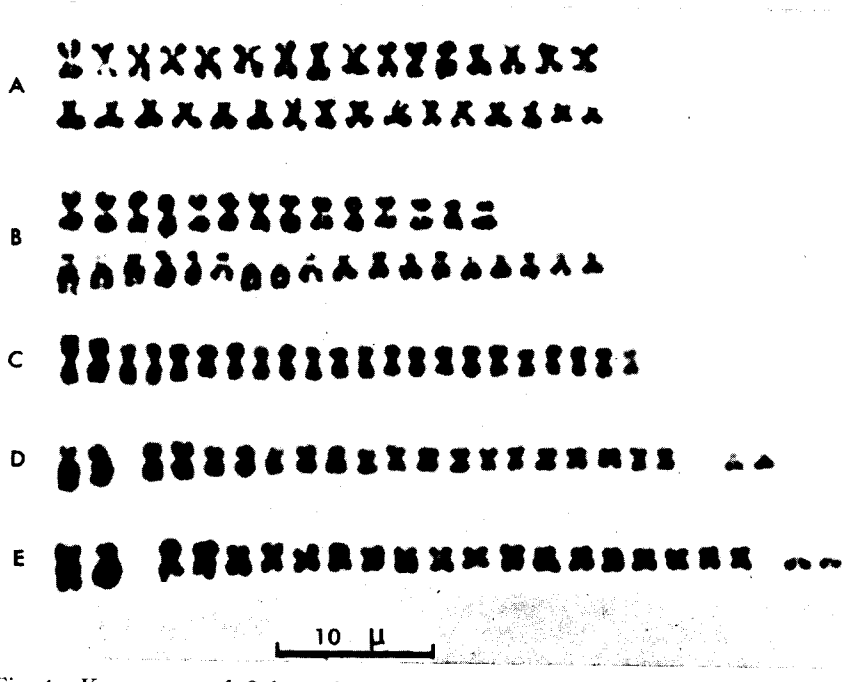

Fig. 4. Karyotypes of *Solenopsis* and *Monomorium* species. A. *S. aurea*, $2n = 32$. B. *S. geminata*, $2n = 32$. C. *S. molesta*, $2n = 22$. D. *M. minimum*, $2n = 22$. E. *M. viridum*, $2n = 22$.

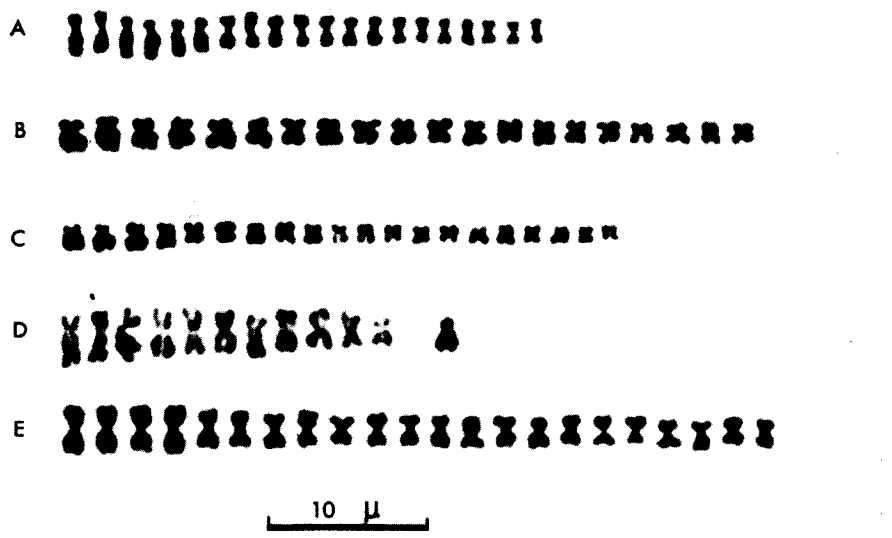

Fig. 5. Karyotypes of species of *Pheidole*, *Leptothorax*, and *Meranoplus*. A. *P. dentata* (Florida), $2n = 20$. B. *P. dentata* (Texas), $2n = 20$. C. *P. dentigula*, $2n = 20$. D. *L. longispinosus*, $n = 12$. E. *M. sp.* (*hirsutus* group), $2n = 22$.

All chromosomes metacentric. Two are slightly larger than the rest, which are medium-sized.

Discussion

Karyotype Relationships Among the Dolichoderinae

Although fewer species of dolichoderines have been examined cytologically than either myrmicines or formicines, rather more points of interest have emerged from dolichoderine cytology than from the cytology of the other two groups. This is because of the greater concentration of effort on the species of one tribe (Tapinomini), instead of a random survey of species, and the generally more detailed descriptions of dolichoderine karyotypes compared with those of karyotypes of species in other subfamilies (Table I).

The Australian species of *Iridomyrmex* fall into four chromosomal groups (Crozier, 1969a; Table I). Most have $n = 9$, with six large to medium-sized metacentric chromosomes and three small acrocentric to subacrocentric chromosomes. Clearly related to these by a centric fusion or dissociation ('Robertsonian' change) are two 8-chromosome species, with seven large to medium-sized metacentric chromosomes and one small acrocentric. This karyotypic difference is correlated with an external morphological character – the position of the eye along the long axis of the head. Another species, *I. glaber*, has $n = 14$, and this striking difference in karyotype is correlated with various morphological differences. *I. itoi*, believed by Brown (1958) conspecific with *I. glaber*, has a similar 14-chromosome karyotype (Imai, *in litt.*). I suspect that these species are not closely related to other *Iridomyrmex*, but instead are the

reduced end of a morphocline including the related genera *Turneria* and *Froggattella;* karyotypes of these genera might help settle this point. Another Australian *Iridomyrmex*, presently unnamed, has $n = 7$, with six large metacentric chromosomes and one small acrocentric; this also differs morphologically from the 8- and 9-chromosome species, and so I believe it is not part of the same system.

An unexpected finding was that *I. humilis* (the Argentine ant), an introduced pest in Australia, has a karyotype similar to that of the Australian 8-chromosome species. The *humilis* karyotype, however, differs from the other 8-chromosome karyotypes in having a large submetacentric that stands out from the rest, and in having one of the other metacentrics noticeably smaller than the rest. The *humilis* karyotype resembles that of the other Neotropical *Iridomyrmex* species in having the large submetacentric, but differs markedly in lacking an extra small acrocentric. Further investigation may show whether the *humilis* karyotype is closely related to the Australian 8-chromosome ones, or whether the resemblance is due to chance.

Because the Neotropical *Iridomyrmex* species resemble those of *Forelius* in external morphology, it might be suggested that the change from $n = 8$

TABLE I
Chromosome numbers in Dolichoderinae

Species (by tribe and genus)	Haploid no.	Source
Dolichoderini		
Dolichoderus		
scabridus	14	Crozier (1966)
Tapinomini		
Bothriomyrmex		
sp.	11	Hauschteck (1963)
Dorymyrmex		
bicolor	13	Crozier (this work)
?pulchellus	9	Crozier (1968a, this work)
?thoracicus	9	Crozier (this work)
Forelius		
foetidus	16	,, ,,
Iridomyrmex (Old World)		
'detectus' group	9	Crozier (1968b, 1969a)
3 spp.	9	,, (1969a)
gracilis (race A)	9	,, ,,
gracilis (race BC)	9	,, ,,
mattiroloi	9	,, ,,
itinerans	8	,, ,,
nitidus	8	,, ,,
sp.	7	,, ,,
glaber	14	,, ,,
itoi	14	Imai and Yosida (1964)
Iridomyrmex (New World)		
pilifer	9	Crozier (this work)
sp. nr. *pilifer*	9	,, ,,
humilis	8	,, (1969a)
Tapinoma		
melanocephalum	5	Crozier (unpublished)
sessile	8	,, ,,
Technomyrmex		
albipes	9	,, (1969a)

(*I. humilis*) to $n = 16$ (*F. foetidus*) has been through polyploidy. This is clearly not so, because whereas metacentric chromosomes predominate in the 8-chromosome karyotype, acrocentrics predominate where $n = 16$. This case clearly illustrates the importance of studying chromosome morphology as well as making chromosome number counts.

The similarity of karyotype between the morphologically dissimilar *Dorymymex ?pulchellus* and *D. ?thoracicus*, and the dissimilarity between the extremely similar, deserticolous, *D. bicolor* and *D. ?thoracicus* illustrate well the potential value of karyotype analyses at the species-group level. The two 9-chromosome species are both Neotropical, while *D. bicolor* is Nearctic. The two karyotypes, however, can be related by four Robertsonian changes, although some further pericentric inversions or other centromere-moving structural changes must have occurred, since some *bicolor* chromosomes are subacrocentric, rather than acrocentric as would be required under current views of the centric fusion or dissociation processes.

In addition to a centromere position polymorphism in *Tapinoma sessile* (Crozier, unpublished), two other cases of intraspecific karyotype variation have been found in dolichoderines. In *Iridomyrmex* of the '*detectus*' group this variation may be between populations (Crozier, 1968b), but in one 'race' of *I. gracilis* there is a polymorphism for centromere position, with one large metacentric being replaced by an acrocentric (Crozier, 1969a). In all these cases the changes are probably due to pericentric inversions, but in the absence of observations on pairing behavior it is possible that centromere shifts have occurred. Since, however, centromere shifts involve three-break rearrangements, while pericentric inversions require only two, the latter seem more probable as the explanation of the observed changes.

On the Supposed Thelytoky of Oecophylla *Species*

Ants of the genus *Oecophylla* have the unique habit of using their larvae as living tools in the construction of arboreal nests fashioned of leaves, and it is doubtless this, their prominence in local faunas, and their economic importance that have led to their being studied by a number of workers in different parts of the world. Unfortunately, no two authors agree on all details of behavior and life history of this ant, even when they have studied ants from the same general locality. Some of these disagreements are minor, but Ledoux (1950, 1954) and Bhattacharya (1943) found that thelytoky occurs in Ivory Coast and Calcutta populations, while Way (1954) and Vanderplank (1960), both working in Zanzibar, and I, studying Malaysian specimens, found no evidence of thelytoky. Both Ledoux (1950, 1954) and Bhattacharya (1943) report that queenless colony fragments can survive and increase in size, while Way (1954), Vanderplank (1960) and I found that such fragments die out. Both Ledoux and Bhattacharya found that worker-laid eggs generally yield workers, whereas I have seen only males arising from worker-laid eggs.

Ledoux (1954) found that worker-laid eggs are generally smaller than queen-laid eggs (0.6 mm long as against 1.1 mm), and yield workers or perhaps queens, but under suitable trophic conditions are the same size as queen eggs and yield males. He reports seeing two polar bodies in large eggs, but none in the small eggs, suggesting that an ameiotic thelytoky takes place in the latter. Since his chromosome count ($n = 12$) differs from mine, a reinvestigation of

the population he studied, using more recent techniques, could be fruitful, especially in view of his own expressed uncertainty on the chromosome number.

Bhattacharya (1943) also found size differences in the eggs of workers and queens, but of a different sort from those reported by Ledoux (1950, 1954). Bhattacharya found that worker-laid eggs and 'fertilized eggs' (eggs from inseminated queens) are about 0.5 mm long, while "the unfertilized eggs of the queen" (eggs from virgin queens) were "much larger," and suggested that the greater size of the latter is due to longer retention in the oviduct. Longer maturation might indeed lead to increased egg size in virgin queens, but longer retention in the oviduct in some other Hymenoptera (e.g., *Nasonia vitripennis* (King, 1962)) leads to egg resorption, and so his explanation seems unlikely. Bhattacharya also found that suitable trophic conditions lead to the appearance of sexual castes in laboratory colonies.

Both Bhattacharya and Ledoux report that queens may be adopted by queenless colony fragments, and Ledoux states that queens cannot found colonies alone, but that groups of workers can. Vanderplank and Way, however, both found that lone queens can found new colonies (Vanderplank includes photographs of such queens) and that colonies, while polydomous, are monogynous (possess but one queen). Vanderplank found that colonies cannot be fused, nor will they accept new queens.

The inconsistencies between the various accounts indicate that further study, especially of those populations in which thelytoky has been reported, is required. In particular, greater care should be taken to prevent accidental inclusion of queens in 'queenless' worker groups; there is evidence that this may have taken place in some of Bhattacharya's experiments.

The possibility remains that the discrepancies between the different accounts of the biology of *Oecophylla* are due to actual differences between the widely separated populations. Differing tendencies toward thelytoky from one population to another are known in many animal species, including some Hymenoptera (e.g., *Apis mellifera*, see Tucker, 1958). *Oecophylla* is currently regarded as having two species, but there is extensive geographic variation in these (see Cole and Jones, 1948) and possibly there are really a number of species, with differing tendencies toward thelytoky, instead of just the presently recognized *O. smaragdina* and *O. longinoda*.

Finally, cases of thelytoky have been reported rather more commonly among formicine ants than among those of other subfamilies, so that its occurrence in *Oecophylla* is not completely improbable. There is no report of the mechanism of thelytoky for any case except for Ledoux's (1954) finding of ameiotic thelytoky in *Oecophylla*. Leutert (1965) however, found, in rearing successive groups of *Lasius flavus*, that the second thelytokously-produced generation is much smaller and feebler than the first. Although he interpreted this effect as due to environmental differences during development, it is better explained as being due to increasing homozygosity associated with a meiotic form of thelytoky.

Karyotype Relationships Among the Formicinae

The tribe Formicini is so far the most uniform one studied in terms of chromosome number, bearing in mind the number of species examined (Table II). All species have either $n = 26$ or $n = 27$. The karyotypes, according to

TABLE II
Chromosome numbers in Formicinae

Species (by tribe and genus)	Haploid no.	Source
Formicini		
Formica		
japonica	27	Imai (1966)
montana	27	Hung (1969)
obscuripes	26	,, ,,
sanguinea	26	Imai (1966)
subintegra	26	Hung (1969)
ulkei	26	,, ,,
yessensis	26	Imai (1966)
Polyergus		
samurai	26 7	,, ,,
Myrmelachistini		
Brachymyrmex		
sp.	9	Crozier (this work)
Lasiini		
Prenolepis		
imparis	8	Hauschteck (1962)
Lasius (*Lasius*)		
alienus	14	,, ,,
pallitarsis	14	Hung (1969)
emarginatus	15	Hauschteck (1962)
niger	15	,, ,, and Imai (1966)
Lasius (*Dendrolasius*)		
fuliginosus	14	Hauschteck (1962)
Lasius (*Cautolasius*)		
talpa	15	Imai (1966)
Lasius (*Chthonolasius*)		
flavus	15	Imai (1966)
nearcticus	15	Crozier (this work)
umbratus	15	Hauschteck (1962); Hung (1969)
Camponotini		
Camponotus		
sp.	9	Imai (1966)
compressus	10	Kumbkarni (1965)
japonicus	14	Imai (1966)
kiusiuensis	14	,, ,,
lateralis	14	Hauschteck (1962)
ligniperda	14	,, (1961)
vagus	14	,, ,,
Camponotus (*Colobopsis*)		
sp. (*impressus* gp.)	26	Crozier (this work)
Oecophylla		
longinoda	?12	Ledoux (1954)
smaragdina	8	Crozier (this work)
Polyrhachis		
rastellata	21	,, ,,

Imai's (1966) photographs, include both metacentric and submetacentric to acrocentric elements.

Listing the subgenera of *Lasius* in Table II reveals that present subgeneric lines are not concordant with chromosome number groups. The subgenus *Lasius* contains both 14- and 15-chromosome species, with both numbers also occurring in species in other subgenera. As noted in this paper, *L. nearcticus*,

a 15-chromosome species, has 14 acrocentrics and one metacentric, with the metacentric smaller than the largest acrocentric. Hauschteck (1962) found that the 14-chromosome species studied by her possess a distinctly larger member of their karyotype, a feature not seen in the 15-chromosome *Lasius* species she studied nor in *L. nearcticus*. *L. niger* appears to have a karyotype similar to that of *L. nearcticus*, according to one of Imai's (1966) photographs.

The subgenus *Colobopsis* of *Camponotus*, as *Camponotus* was formerly divided, comprises species that typically nest in wood and have soldiers with modified heads to serve as 'doorstoppers'. Some species, if not all, pupate without cocoons, whereas other *Camponotus* species pupate in cocoons. Due to the morphological modifications of the soldier's head, and the biological features noted above, *Colobopsis* remains a distinct group, whereas subgeneric lines elsewhere in *Camponotus* have become impractical and hard to justify. Perhaps a further character separating *Colobopsis* will prove to be chromosome number, because *Colobopsis* sp. has $n = 26$, whereas all other species of *Camponotus* cytologically examined have haploid numbers of 14 or less. According to Imai's (1966) photographs, *Camponotus* sp. ($n = 9$) has apparently all chromosomes metacentric, while some submetacentrics and acrocentrics occur in the karyotype of *C. kiusiuensis* ($n = 14$). *Colobopsis* sp. ($n = 26$, this paper) has, as might be expected, most chromosomes acrocentric.

Karyotype Relationships Among the Ponerinae

As can be seen from Table III, only six species of Ponerinae have been examined cytologically, so that it is not surprising that, apart from a chromosome number polymorphism in the Australian species *Rhytidoponera metallica*, no features of particular interest have yet been found in this group. The high numbers found in some species are, however, significant because of the basal position of the subfamily in all phylogenetic schemes. In Brown's (1954) arrangement, for example, the Ponerinae are the stem subfamily to one of the two complexes into which he divides the Formicidae.

TABLE III
Chromosome numbers in Ponerinae and Myrmeciinae

Species (by tribe and genus)	Haploid no.	Source
Ponerini		
Brachyponera luteipes	11	Imai and Yosida (1964)
Cryptopone sauteri	14	,, ,, ,, ,,
Ectatommini		
Proceratium silaceum	18	Crozier (this work)
Rhytidoponera metallica	12–22	,, (1969b)
tasmaniensis	23	,, ,,
victoriae	21	,, ,,
Myrmeciini		
Myrmecia ruginoda	15	,, (1966)

Southern Victorian populations of *Rhytidoponera metallica* have $n = 22$ to 17, with progressive replacement of two acrocentrics at a time with a metacentric to yield numbers lower than 22 (Crozier, 1969b). A further collection with $n = 12$ represents either a further reduction in this Robertsonian system, or a sibling species. Since related species of *Rhytidoponera* have high numbers, it is more likely that the *R. metallica* karyotypes arose by centric fusions from a higher-numbered karyotype than by 'fissions' from a lower-numbered one.

Karyotype Relationships Among the Myrmicinae

With haploid numbers ranging from 4 to 28, the Myrmicinae include the extremes of chromosome number in ants. This undoubtedly is a reflection not only of the great number of species and the heterogeneity of this subfamily, but also of the fact that more species of myrmicines have been examined cytologically than of any other ant subfamily. The known chromosome numbers are given in Table IV. The present tribal arrangements in this subfamily are somewhat chaotic and this is perhaps reflected in the wide variations of chromosome number in some tribes.

Karyotype variation in *Aphaenogaster rudis* (Crozier, unpublished) suggests that in some species karyotype change can be rapid relative to phenotypic change. This could explain the cases where fairly closely related species have karyotypes that cannot easily be related. Two of these cases are the two *Meranoplus* karyotypes known and those of the dacetines *Cobostruma alinodis* and *Epopostruma* sp. In both cases one species has 10 metacentric chromosomes, while the other has 11, simple Robertsonian changes thus not being a suitable explanation. Another case involves *Pheidole* species with 9 and 10 chromosomes, all chromosomes in each case being metacentric.

Large solenopsidine species (*Solenopsis aurea* and *S. geminata*) have $n = 16$, while the other, smaller species (e.g., *Monomorium pharaonis* and *S. molesta*) have $n = 11$. The apparent close similarity between the small *Monomorium* and *Solenopsis* species is, however, spurious, as the karyotypes differ, with the *Monomorium* karyotypes having a small acrocentric, whereas all the *Solenopsis molesta* chromosomes are medium-sized metacentrics.

Myrmica species typically have high numbers (Hauschteck, 1965). In *M. sulcinodis*, with $n = 28$, many cells in the testes were found to have only 14 'chromosomes' (Hauschteck, 1965). These results are reminiscent of those obtained by Kerr and Araujo (1957) for some bees, where one species with $n = 18$ has apparent pairing of chromosomes in the testes (only 9 bodies are seen at meiotic prophase, the full 18 being seen in later stages). It is thus possible that *M. sulcinodis* is evolutionarily tetraploid, but no possible ancestral karyotype has yet been found, whereas in the trigonid case a series of bees related to the $n = 18$ species have $n = 9$. A possible alternative explanation of the *M. sulcinodis* case is that telomere exchanges have occurred in the evolution of this karyotype, resulting in homologous terminal segments on non-homologous chromosomes. This mechanism has been invoked to explain non-homologous chromosome association in the grasshopper *Austroicetes interioris* (Nankivell, 1967). Nankivell suggests that telomere exchanges might be common in evolution, but that misparing is usually suppressed except in unusual circumstances.

TABLE IV
Chromosome numbers in Myrmicinae

Species (by tribe and genus)	Haploid no.	Source
Crematogastrini		
Crematogaster		
laboriosa	13	Imai (1966)
Dacetini		
Colobostruma		
alinodis	11	Crozier (1968c)
Epopostruma		
sp.	10	,, ,,
Orectognathus		
clarki	15	,, (1966, 1968c)
Leptothoracini		
Leptothorax		
longispinosus	12	,, (this work)
spinosior	12	Imai (1966)
tuberum	9	Hauschteck (1961)
Meranoplini		
Meranoplus		
sp. (*oceanicus* gp.)	10	Crozier (1966)
sp. (*hirsutus* gp.)	11	,, (this work)
Myrmecinini		
Pristomyrmex		
pungens	12	Imai (1966)
Myrmicini		
Myrmica		
laevinodis	24	Hauschteck (1965)
sulcinodis	28	,, ,,
Pheidolini		
Pheidole		
sp. (*concentrica* gp.)	9	Crozier (1966)
dentata	10	,, (this work)
dentigula	10	,, ,,
fervida	10	Imai (1966)
pallidula	12	Hauschteck (1961)
Aphaenogaster		
famelica	17	Imai (1966)
sp.	16	,, ,,
rudis	16–18	Crozier (unpublished)
subterranea	11	Hauschteck (1962)
Messor		
aciculatum	22	Imai (1966)
Stenamma		
brevicorne	4	Hauschteck (1962)
Solenopsidini		
Monomorium		
minimum	11	Crozier (this work) ;
pharaonis	11	Imai (1966); Smith and Peacock (1957)
viridum	11	Crozier (this work)
Solenopsis		
aurea	16	Crozier (this work)
fugax	11	Hauschteck (1961)
geminata	16	Crozier (this work)
molesta	11	,, ,,
sp.	11	,, (1966)

TABLE IV (Continued)

Species (by tribe and genus)	Haploid no.	Source
Tetramoriini		
Strongylognathus		
huberi	14	Hauschteck (1962)
Tetramorium		
caespitum	14	,, (1961); Imai (1966)
Tribe uncertain		
Vollenhovia		
emeryi	18	Imai (1966)

Cytogenetic Aspects of Zoogeography and Phylogeny in Ants

Imai (1966) has put forward two interesting ideas bearing on ant karyotype evolution and cytogeography. First, he suggests that, while the Myrmicinae have evolved through 'heteroploid' changes, polyploidy has occurred in the evolution of the Formicinae. This conclusion is based on the range of chromosome numbers as known to him at that time, which he claims fall into three groups. These groups, however, are rather indistinct; furthermore the two 'gaps' in chromosome number in the Formicinae have been bridged by recent discoveries. Within his suggested polyploid series there are no exact multiples of any basic number. In fact, therefore, chromosome morphology and other data are more consistent with hypotheses involving Robertsonian changes than with any involving polyploidy, because there is generally an increase in the proportion of acrocentrics per karyotype with increase in haploid number in ants – the '*nombre fondamentale*' is less variable than haploid number.

The second suggestion Imai (1966) makes is that unusually high numbers in ants tend to occur more frequently in species living in 'high' latitudes, or harsh environments, than in those living in 'low' latitudes or favourable environments. While it is not feasible to examine the ecology of each species cytogenetically examined to determine the harshness of its environment, it is easy to examine the simple relationship between chromosome number and latitude. A correlation coefficient of chromosome number against latitude was calculated, with each locality assigned to latitudinal bands centered at 5°, 15° etc., using the counts given in Tables I to IV. Each number in a genus was counted once for each latitude band in which it has been found. By counting each number in a genus only once per latitude band, regardless of the number of species actually involved, I attempted to reduce the bias introduced by different intensities of sampling in different genera. A value of $r = 0.1203$ was obtained which is not significant at the $P = 0.1$ level. It therefore does not appear that there is a simple relationship between chromosome number and latitude in ants.

Based on the chromosome numbers given in Tables I to IV, counting each number once per genus, the mean chromosome number in ants is $n = 14.4$, with the median being $n = 14$.

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