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Karyological survey of Indian ants

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ABSTRACT

The karyotypes of 94 species of Indian ants were examined. Their chromosome numbers range almost continuously between $n=5$ and 38, though the frequency distribution is bimodal with a remarkable antimode at $n=11$ and two modal points at $n=10$ and 15. Based on this bimodal distribution, Indian ants were classified into two groups: Lower-numbered species ($n\leq 11$) and higher-numbered species ($n>11$), the former being characterized by metacentric-rich karyotypes, and acrocentrics predominate in the latter. The three major subfamilies (Ponerinae, Myrmicinae, and Formicinae) showed a highly divergent distribution in chromosome number, ranging between $n=$ 7–38, 6–35, and 8–27, respectively, suggesting a convergence in karyotype evolution of each subfamily, Another three subfamilies, of which only a few species were examined, had moderate or lower numbers, i.e., $n=5$–14 in Dolichoderinae, $n=14$ in Cerapachyinae, and $n=12$ in Dorylinae. We found four Robertsonian polymorphisms, two pericentric inversion polymorphisms, and four reciprocal translocations, three of which were fixed. Robertsonian polymorphisms were found only in higher-numbered species, while translocations were restricted to lower-numbered species. A possible biological significance for this nonrandom distribution of rearrangements is discussed with reference to karyotype evolution in ants.

1. INTRODUCTION

Animal karyotype evolution has generally been analyzed by the following procedures; (1) detection of chromosome rearrangements by comparison of karyotypic homologies among members of a given genus, and (2) reconstruction of a possible evolutionary pathway of karyotype alteration based on a

directionality of chromosome rearrangements identified. This conventional method has, however, some fundamental problems. The most serious problem is that chromosome rearrangements contributing to animal karyotype evolution (e.g., Robertsonian rearrangement and pericentric inversion) are in a qualitative sense bidirectional. Needless to say, Rebertsonian rearrangement involves centric fusion and centric fission, of which the former changes two acrocentrics into one metacentric (2A→1M) and the reverse by the latter. In the same manner, two opposite inversions altering 1A→1M and 1M→1A (denoted as p.i. (AM) and p.i. (MA), respectively) are theoretically possible (for details see Imai and Crozier 1980). Historically, centric fusion has long been considered to be the major type of rearrangement in animal karyotype evolution (e.g., White 1973). This is the so-called fusion hypothesis. The majority of centric fusions claimed have, however, been interpreted only conforming to the fusion hypothesis, but not on solid evidence. Indeed, it is practically difficult in many cases to determine which of the opposite rearrangements mentioned above has actually occurred in each case. The second problem is associated with karyotypic homology, i.e., the conventional method is less successful for a quantitative analysis of karyotype evolution at taxonomic levels higher than genus, because karyotypic homology is obscure at the family or order level. Even if there is a homology, to compare several hundreds or thousands of karyotypes involved in each family or order is highly impracticable. These problems will be solved, if chromosome rearrangements are in a statistical sense uni-directional, and if it is possible to devise a new method that can describe chromosome morphologies and also karyotypes quantitatively without omitting information about chromosome rearrangements that have contributed to animal karyotype evolution.

The senior author has shown that the centromere distributes nonrandomly on mammalian chromosomes, and that chromosome morphologies can be described quantitatively and classified into three biologically significant categories: T (telocentric), A (acrocentric), and $\overline{M}$ (metacentric in a broad sense, including conventional M, SM, or ST) (Imai 1975, 1976). This finding provides a quantitative approach to karyotype evolution at higher taxonomic levels, such as family or order, and a number of fruitful findings have been accumulating. Imai and Maruyama (1978) suggested that pericentric inversion is stochastically unidirectional, i.e., p.i. (AM) occurs more frequently than p.i. (MA). Imai (1978) proposed a cyclical chromosome alteration model based on a theoretical analysis of the origin of telocentrics, i.e., $\underline{\rightarrow T \rightarrow A \rightarrow \overline{M} \rightarrow}$, in which T→A changes by tandem growth of constitutive heterochromatin in short arms (t.g.c.h.), A→$\overline{M}$ mainly by p.i. (AM) and less often by centric fusion or t.g.c.h., and $\overline{M}$→T by centric fission. Note that centric fusions are considered in this model as occasional 'back eddies'. This line of theoretical

approach has recently been combined with the karyograph method devised by Imai and Crozier (1980).

The karyograph is a two dimensional graph on which karyotypes are plotted in terms of chromosome number ($2n$) versus arm number ($2AN$), where $2AN$ is determined by counting one for each A or T and two for each $\bar{M}$ chromosomes. Robertsonian rearrangements alter chromosome number while leaving arm number constant, and pericentric inversions do the reverse. Hence, density distributions of karyotypes on the graph carry information about the kinds of rearrangements contributing to karyotype evolution. This means in other words that the karyograph method is highly valuable for a quantitative analysis of karyotype evolution at the family or ordinal level, at least in mammals (Imai 1983; Imai *et al.* 1983).

We are interested in determining whether or not the quantitative approach to karyotype evolution developed for mammals is also applicable to ants (Insecta; Hymenoptera: Formicidae), which are phylogenetically quite distinct from mammals. Cytogenetics of ants has greatly advanced during the last two decades, and about two hundred ant species have been karyotyped (see papers by Hauschteck (1961, 1962, 1965), Imai (1966, 1969, 1971, 1974), Imai and Kubota (1972, 1975), Imai *et al.* (1977), and Crozier (1968a,b,c, 1969, 1970 a,b, 1977). We need, however, further accumulation of karyological data (at least 500 ant species, and if possible 1,000) for the present purpose. Taking these circumstances into consideration, the present paper deals with the karyotypes of a total of 94 Indian ant species, and discusses the possible biological significance of the nonrandom distribution of Robertsonian and translocation polymorphisms found in ants.

2. MATERIALS AND METHODS

A total of 186 colonies of Indian ants were collected from the 15 localities listed in Table 1, which represent north, east, west and south India. The collections were made from August to October in 1978 by the senior author, and the colonies collected were labeled as HI78-(1-186).

Chromosome preparations were made in most cases from the cerebral ganglia of worker prepupae (genetically females) applying an air-drying technique developed by Imai *et al.* (1977). Testes of early male pupae were also used if they were available. The procedure of chromosome preparation used by Imai *et al.* (1977) was partly modified in the steps (6) and (7) as follows; (6) *after 30 sec or one min* (i.e., just before the cell suspension dries) add two drops of freshly-prepared Fixative II (1:1 acetic ethanol), *causing the Fixative I (60% 1:1 acetic-ethanol) to move to the margin of the slide. After 15-30 sec, remove the Fixative I with absorbent filter paper.* (7) *After one or two min* (i.e., *just* before the preparation dries) add two drops of

Table 1. *Localities and codes of Indian ants used in this study*

Code(s) of colony HI78–	Locality
1–20, 24, 25, 30–40, 44–46, 48–56, 64	Campus of Punjab University, Section 14, Chandigarph, Panjab
21–23, 26–29	Government Nursery, Section 23, Chandigarh, Panjab
41–43	Simla, Himachal Pradesh
47	Pinjore, Panjab
57–63, 65	Dehra Dun, Uttar Pradesh
66–71, 76, 81	Indian National Science Academy, New Delhi, Uttar Pradesh
72, 73–75, 77–80	Zoological Garden, New Delhi, Uttar Pradesh
82–85, 93–104, 110, 111	Central Tasar Research Station, Ranchi, Bihar
86–92	Hundru Falls, Ranchi, Bihar
105–109, 112	Amalia Forest, Ranchi, Bihar
113–117	Campus of Calcutta University, Calcutta, West Bengal
118–140	Botanical Garden, Calcutta, West Bengal
141–145, 147–153	Maharashtra Association for the Cultivation of Science, Poona, Maharashtra
146, 154–173	Mahabaleshwara, Maharashtra
174–186	University of Mysore, Mysore, Karnataka

Fixative III (glacial acetic acid). *After 15–30 sec, remove the Fixative II and III, which have moved to the margin of the slide, with filter paper*, and allow it to dry completely. (The modified parts are represented by italics). The best results were obtained with room temperature at 20–25°C and relative humidity about 65±5%.

For describing chromosome morphologies, we use here $\bar{A}$ (acrocentric in a broad sense, which involves conventional T and A) and $\bar{M}$ (metacentric in a broad sense, i.e., a general term for M, SM, or ST). This classification system is useful for estimating arm number (AN or $2AN$) as proposed by Imai and Crozier (1980). Our present system is, however, somewhat arbitrary or subjective (especially for the discrimination between ST and A), because the non-random localization of the centromere found in mammals (Imai 1975), by which chromosomes can be classified into two biologically significant categories $\bar{A}$ and $\bar{M}$, is not yet known to occur in ants. However, the evidence that more than 90% of (A or T) and (M, SM, or ST) chromosomes identified by mammalian cytogenetics correspond respectively to $\bar{A}$ and $\bar{M}$ (Imai 1973) suggests that our tentative estimation of arm number may still be valuable for analyzing the rough outline of ant karyotypes.

The locality code, cytological details, and figure references for each colony studied are listed in Table 2. Identification of species was made by Baroni Urbani and Kubota. One complete set of dry and alcohol specimens of these Indian ants are preserved by Kubota, and another set of dry specimens is

Table 2. *Karyological data of Indian ants: Males are in parentheses and others are workers*

Taxon	Chrom. number (n), 2n	Arm number (AN), 2AN	Ind. no. obs.	Modal cell no. obs.	Figs.	Colony HI78–
Subfamily PONERINAE						
Leptogenys						
hysterica	26	52	1	8	1 a	74
sp. 5 (near *peuqueti*)	30	60	5	17		154
	(15), 30	(30), 60	(1), 2	(7), 8	(1 b)	158
diminuta (var. *leviceps*)	38	50	5	16	1 c	57
ocellifera	46	80	4	14	1 d	87
minchini	52	58	1	3	1 e	126
Anochetus						
madaraszi	28	48	2	5	2 a	128
yerburyi	30	51	3	32	2 b	82
graeffei	30	51	2	12	2 c	81
	30	51	2	5		129
	30	51	3	7		130
sp. 4	30	53	1	9	2 d	67
sp. 5	34	51	1	4	2 e	143
Bothroponera						
sp. 1 (near *tesserinoda*)	48	48	9	46	3 a	13
rufipes	48	68	1	2	3 b	125
sp. 2 (near *tesserinoda*)	52	66	1	8	3 c	98
rubiginosa	76	94	2	3	3 d	105
Centromyrmex						
feae	44	58	5	16	4 a	118
Diacamma						
vagans	(7)	(14)	(2)	(19)		121
	14	28	4	31	4 b	174
	(7), 14	(14), 28	(1), 1	(4), 1		175
sp. 2	30	58	2	6	4 c	181
Ectomomyrmex						
sp.	38	54	4	19	4 d	86
Brachyponera						
luteipes (=*obscurans*)	22	42	7	58		21
	22	42	3	13		41
	22	42	4	22		58
	22	42	4	29	5 a	73
Odontoponera						
transversa	46	60	2	4	5 b	47
Subfamily CERAPACHYINAE						
Cerapachys						
biroi	28	53	5	9	5 c	119
	28	53	5	14		127

(to be continued)

Table 2. (*Continued*)

Taxon	Chrom. number (n), 2n	Arm number (AN), 2AN	Ind. no. obs.	Modal cell no. obs.	Figs.	Colony HI78-
Subfamily MYRMICINAE						
Cardiocondyla						
nuda	28	36	2	13	5 d	48
Meranoplus						
bicolor	16	30	6	39		1
	16	30	7	33	5 e	4
	16	30	5	40		68
	16	30	4	24		92
	16	31	4	19	5 f	99
	Pericentric inversion polymorphism					
	16	30	2	14		131
Crematogaster						
biroi	24	48	59	35	6 a	30
	24	48	2	8		69
brunnea (var. *rabula*)	36	68	5	33	6 b	162
subnuda	(18), 36	(36), 72	(2), 2	(12), 20	6 c	31
	36	68-70	3	14		76
	36	67, 68	4	20		77
	C-band polymorphism in short arms					
rothneyi	50	54	5	21		84
	50	54	1	4		140
	50	54	5	41	6 d	170
Myrmicaria						
brunnea	44	68	5	12		89
	44	68	5	19	6 e	106
Aphaenogaster						
smythiesi	34	50	1	6	6 f	43
beccarii	46	50	5	31		146
	(23), 46	(25), 50	(2), 2	(9), 2	(6 g)	161
Pheidole						
mus	12	24	3	16		164
	12	24	5	55	7 a	166
woodmasoni	18	36	4	29	7 b	5
	18	36	2	7		6
	18	36	5	35		34
	18	36	4	30		46
sp. 14	18	36	2	20	7 c	139
indica	20	40	4	15	7 d	24
rotschana	20	40	4	14		103
	20	40	4	11		148
	20	40	1	1		151
sp. 3	20	40	4	23	7 e	167
sp. 4	20	40	5	27	7 f	62
sp. 8	20	40	3	35	7 g	14
	20	40	4	27		70
	20	40	5	46		93

(to be continued)

Table 2. (*Continued*)

Taxon	Chrom. number (n), 2n	Arm number (AN), 2AN	Ind. no. obs.	Modal cell no. obs.	Figs.	Colony HI78–
sp. 9 (near *fossulata*)	20	40	5	34		9
	20	40	5	51	8 a	15
	20	40	5	54		36
sp. 11	20	40	4	18	8 b	100
sp. 13 (near *watsoni*)	28	44	5	29		33
	28	44	5	16		71
	28	44	2	8	8 c	108
	28	44	2	12		134
sp. 5	30	48	3	16	8 d	101
latinoda	42	?	1	5		27
	42	62	5	18	8 e	66
	42	62	2	11		104
	42	62	5	11		124
	42	62	3	10		142
sp. 1 (near *grayi*)	42	62	5	25	8 f	35
Oligomyrmex						
sp. 5	26	52	5	38	9 a	137
	26	52	3	5		138
sp. 4	(16)	(26)	(1)	(20)	(9 b)	59
	32	?	2	10		109
asinus	44	52	1	2		7
	44	52	4	13	9 c	75
sp. 2	44	70	5	17	9 d	136
Pheidologeton						
diversus	42	54	4	15	9 e	133
Lophomyrmex						
bedoti	38	48	5	42	9 g	60
Trigonogaster						
sp.	24	42	1	5	9 f	112
Monomorium						
dichroum	16	32	4	36	10 a	53
orientale	20	40	3	8	10 b	28
indicum	22	44	4	16	11 e	25
	22	44	4	45	=11 e	40
	21	42	3	25	=11 a, b	45
	21	42	5	69	=11 a	50
	22	44	5	13	=11 e	54
	21	42	4	15	11 a, d	55
	21	42	5	24	11 b, c	56
	21	42	5	18	=11 a	78
	Translocation polymorphism					
sp. 5	34	54	6	18	10 c	2
scabriceps	38	52	8	46		10
	38	52	3	14		12
	38	52	3	23	10 d	20
	38	52	4	31		111

(to be continued)

Table 2. (*Continued*)

Taxon	Chrom. number (n), 2n	Arm number (AN), 2AN	Ind. no. obs.	Modal cell no. obs.	Figs.	Colony HI78–
glabrum	38	66	5	34	10 e	176
sp. 6 (near *glabrum*)	38	68	6	14	10 f	147
latinode	70	80	4	24	10 g	150
Messor						
sp.	41	48	8	45	12 a	49
	Robertsonian polymorphism					
Solenopsis						
geminata	32	62	5	36		88
	32	58	3	10		94
	32	60, 62	4	19		114
	32	58	3	19	12 b	141
	32	58	3	4		185
	C-band polymorphism in short arms					
Tetramorium						
simillimum	14	28	3	35	12 d	39
	14	28	2	9		102
smithi	26	42	5	26	12 c	85
sp. 3	36, 35	45, 44	4	1, 32	13 a , b	163
	35	44	2	3		168
	35	44	2	11	13 c	172
	Robertsonian polymorphism					
Triglyphothrix						
lanuginosa	14	26	4	47	12 e	16
	14	26	5	52		32
	14	26	4	35		178
walshi	14	28	4	44		11
	14	28	3	24	12 f	72
	14	28	1	4		95
Subfamily DORYLINAE						
Aenictus						
brevicornis	24	46	4	14	4 e	64
Subfamily DOLICHODERINAE						
Iridomyrmex						
anceps	18	32	3	7	14 a	96
Tapinoma						
melanocephalum	10	18	1	3	14 b	186
indicum	10	18	5	23		3
	10	18	5	55	14 c	79
	10	18	5	45		156
	10	18	4	39		173
Technomyrmex						
albipes	16	32	5	46	14 d	65
sp. 2 (group *bicolor*)	28	36	6	69	14 e	23
	28	36	4	20		29

(to be continued)

Table 2. (*Continued*)

Taxon	Chrom. number (n), 2n	Arm number (AN), 2AN	Ind. no. obs.	Modal cell no. obs.	Figs.	Colony HI78-
Subfamily FORMICINAE						
Cataglyphis						
setipes	54	64	2	3	14 f	18
Acantholepis						
lunaris	18	34	7	36	15 b	42
sp. 1 (near *sericea*)	18	34	5	59	15 c	51
capensis	18	34	4	21	15 a	107
sp. 2 (near *fergusoni*)	18	34	2	15	15 d	153
Anoplolepis						
longipes	34	42	1	3		144
	34	42	3	20	14 g	177
	34	42	2	11		183
Paratrechina						
longicornis	16	30	5	29	15 e	17
	16	30	3	34		19
	(8), 16	(15), 30	(1), 1	(7), 6		80
	16	30	4	18		116
	16	30	2	6		149
	16	30	2	9		160
sp. 3 (near *yerburyi*)	(15), 30	(15), 30	(2), 2	(5), 12	15 f	117
indica	30	32	3	23	15 g	63
Oecophylla						
smaragdina	16	32	4	16		90
	16	32	4	21	16 a	115
	16	32	5	20		145
Camponotus						
dolendus	20	40	5	17		159
	20	40	4	19	16 c	165
mitis	20	40	3	25	16 d	91
	20	40	3	19		182
sp. 10 (near *infuscus*)	20	40	2	10		155
taylori	24	24	5	27	16 e	120
variegatus	26	52	5	14		152
	26	46	5	28	16 f	171
	C-band polymorphism in short arms					
sp. 7 (near *variegatus*)	32	42	1	2	16 g	38
sp. 12 (near *variegatus*)	34	44	3	8	17 a	157
sp. 9 (near *variegatus*)	34, 35	39, 40	7, 4	17, 13	18	26
	Fission-inversion polymorphism					
crassisquamis	40	40	7	21	17 b	44
	39, 40	40, 40	2, 3	8, 8	17 c	110
	Robertsonian polymorphism					
paria	40	42	1	2		22
	40	42	1	3	17 d	37
	40	42	2	7		123
thraso	40	40	2	9	17 e	184
sericeus	44	46	2	3	17 f	83
Polyrhachis						
simplex	42	48	5	11	16 b	52

maintained by Baroni Urbani. Among the 94 species discriminated in the present study, about one third (32) were unidentifiable species or new species, which we have assigned temporary labels such as sp. 1, 2, etc. Detailed taxonomic descriptions of these will be published by Baroni Urbani in a separate paper. Part of our work was published preliminarily by Imai and Kubota (1982). Since then, a number of species were newly identified by Baroni Urbani. To avoid confusion in nomenclature, we principally use here the species numbers which were used in the previous paper if their scientific names are not yet known. Generic names of the following groups identified by Kubota were revised by Baroni Urbani: *Holcomyrmex* (sp. 1, 2, 3 and 5)→ *Monomorium*; *Holcomyrmex* (sp. 4)→*Messor*; *Ectomomyrmex* (sp. 1 and 3)→ *Bothroponera*; *Ectomomyrmex* (sp. 4) → *Aenictus*; *Trachymesopus* → *Bothroponera*; and *Pheidole* (sp. 15)→*Monomorium*. The species are basically arranged in Table 2 by their chromosome number from low to high-numbered species.

3. RESULTS

1) *Subfamily Ponerinae*

We examined the karyotypes of 20 ponerine ant species belonging to 8 genera (Figs. 1-5, Table 2). Their chromosome numbers distribute fairly uniformly in the range $2n=14$, 22, 28, 30, 34, 44, 46, 48, 52, and 76, with the lowest number being found in *Diacamma vagans* (Fig. 4b) and the highest in *Bothroponera rubiginosa* (Fig. 3d). Some karyological and cytotaxonomic remarks on each genus are summarized below.

Leptogenys: Five species were collected from Dehra Dun, New Delhi, Calcutta and Mahabaleshwara. Their diploid karyotypes ($2K$) are formulated respectively as $2K=26\bar{M}$ for *L. hysterica* (Fig. 1a), $2K=30\bar{M}$ (or $K=15\bar{M}$) for *L. sp. 5* (Fig. 1b), $2K=26\bar{A}+12\bar{M}$ for *L. diminuta* (Fig. 1c), $2K=12\bar{A}+34\bar{M}$ for *L. ocellifera* (Fig. 1d), and $2K=46\bar{A}+6\bar{M}$ for *L. minchini* (Fig. 1e). The chromosome numbers range in this genus between $2n=26$ and 52, while their arm numbers are $2AN=50$-60 excepting *L. ocellifera* ($2AN=80$). This result suggests that karyotype alteration in *Leptogenys* has occurred mainly by Robertsonian rearrangement, though pericentric inversion seems to predominate in *ocellifera*.

Anochetus: Five species were karyotyped. The diploid karyotype of *A. madaraszi* was $2K=8\bar{A}+20\bar{M}$ (Fig. 2a). In the same manner, *A. yerburyi* $2K=9\bar{A}+21\bar{M}$ (Fig. 2b), *A. graeffei* $2K=9\bar{A}+21\bar{M}$ (Fig. 2c), *A. sp. 4* $2K=7\bar{A}$ $23\bar{M}$ (Fig. 2d), and *A. sp. 5* $2K=17\bar{A}+17\bar{M}$ (Fig. 2e). These species, though they were found in northern India along with *Leptogenys*, are karyotypically rather conservative, because both chromosome number and arm number vary

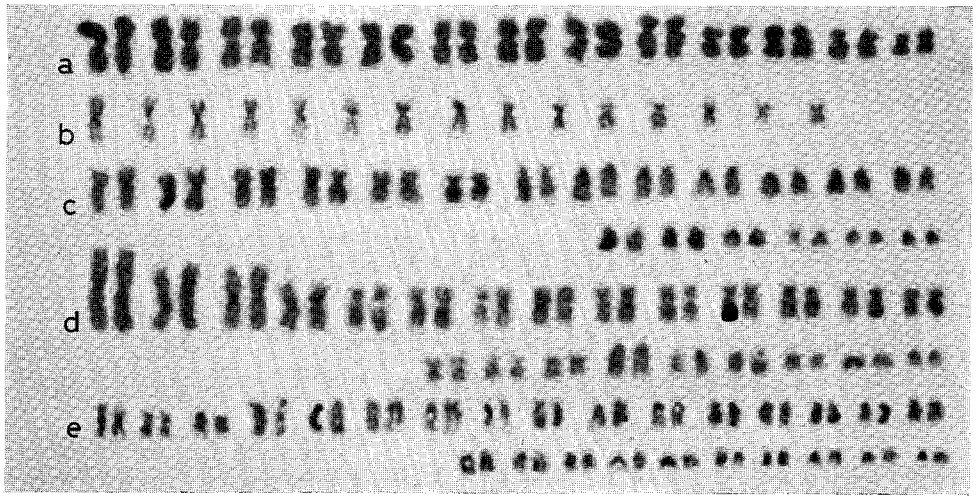

Fig. 1. Karyotypes of ponerine ants (I). a. *Leptogenys hysterica* ($2n=26$). b. *L. sp. 5* ($n=15$). c. *L. diminuta* ($2n=38$). d. *L. ocellifera* ($2n=46$). e. *L. minchini* ($2n=52$).

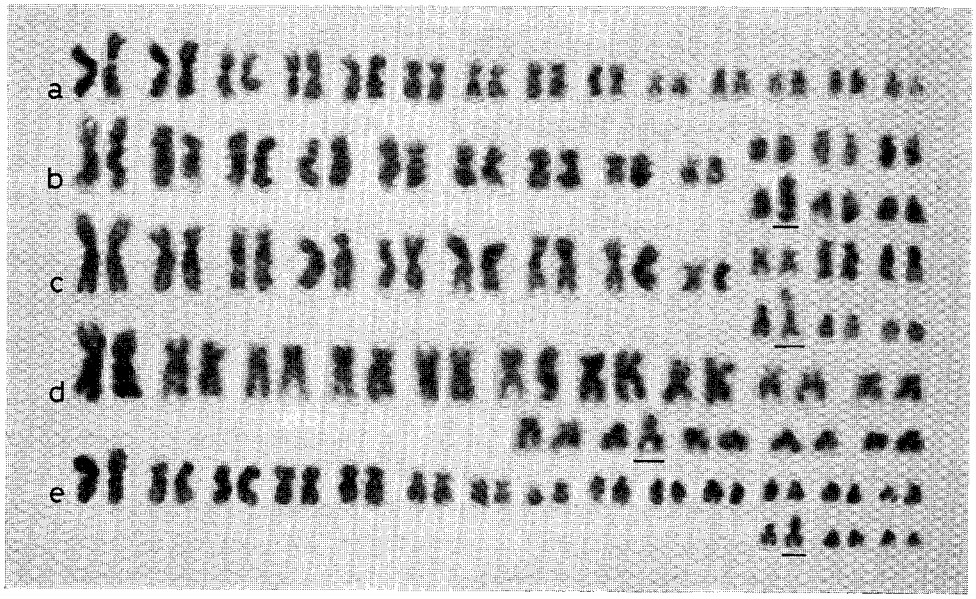

Fig. 2. Karyotypes of ponerine ants (II). a. *Anochetus madaraszi* ($2n=28$). b. *A. yerburyi* ($2n=30$). c. *A. graeffei* ($2n=30$). d. *A. sp. 4* ($2n=30$). e. *A. sp. 5* ($2n=34$).

narrowly ($2n=28$-34 and $2AN=48$-53). Besides, the karyotypes of *A. yerburyi* and *A. graeffei* are identical, and all members excepting *A. madaraszi* have a a common marker chromosome with enlarged heterochromatic short arm (see underlines in Fig. 2). Three colonies of *A. graeffei* which were collected from New Delhi and Calcutta showed the identical karyotype $2K=9\bar{A}+21\bar{M}$.

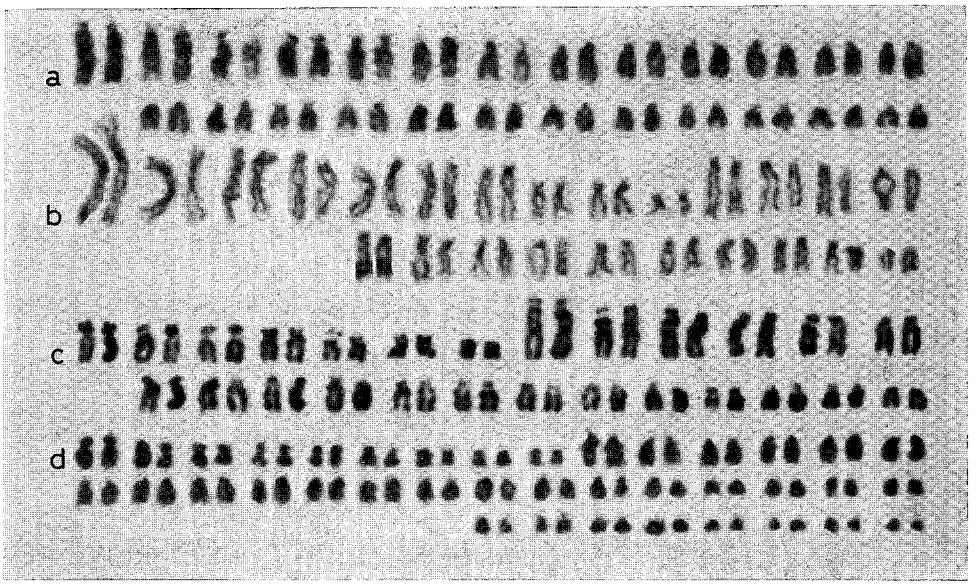

Fig. 3. Karyotypes of ponerine ants (III). a. *Bothroponera sp. 1* ($2n=48$). b. *B. rufipes* ($2n=48$). c. *B. sp. 2* ($2n=52$). d. *B. rubiginosa* ($2n=76$).

Bothroponera: The genus *Bothroponera* is placed by W. L. Brown, Jr, as a synonym of *Pachycondyla* (Maschwitz *et al.* 1981). However, we use here *Bothroponera* as an independent genus, because the senior author already used the genus name *Bothroponera* in his previous paper (Imai *et al.* 1977), and because the revision of this genus is not published yet. Four species of *Bothroponera* were examined (Fig. 3). Both *sp. 1* and *sp. 2* are morphologically similar to *B. tesserinoda*, though they are karyotypically distinct from each other, i.e., $2K=48\bar{A}$ in the former (Fig. 3a) but $2K=38\bar{A}+14\bar{M}$ in the latter (Fig. 3c). *B. rufipes* ($2K=28\bar{A}+20\bar{M}$, Fig. 3b) has the same chromosome number as *B. sp. 1* ($2n=48$) but the two species differ in arm number ($2AN=68$ and 48, respectively). *B. rufipes* has a peculiar defence mechanism: workers release long white streams of foam when they are seized with forceps. The same phenomenon was already reported in the Malaysian species *tridentata* by Maschwitz *et al.* (1981) and other authors. Karyotypes of these three *Bothroponera* species may have evolved mainly by pericentric inversion, for their arm numbers fluctuate ($2AN=48$–66) rather considerably more than chromosome number ($2n=48$–52). On the other hand, Robertsonian rearrangement as well as pericentric inversion would have contributed to produce the karyotype of *B. rubiginosa* ($2K=58\bar{A}+18\bar{M}$; Fig. 3d), which has the highest chromosome number ($2n=76$) and arm number ($2AN=94$) in the present study.

Centromyrmex: One colony of *C. feae* was collected from Calcutta, of which the karyotype formula is $2K=30\bar{A}+14\bar{M}$ (Fig. 4a).

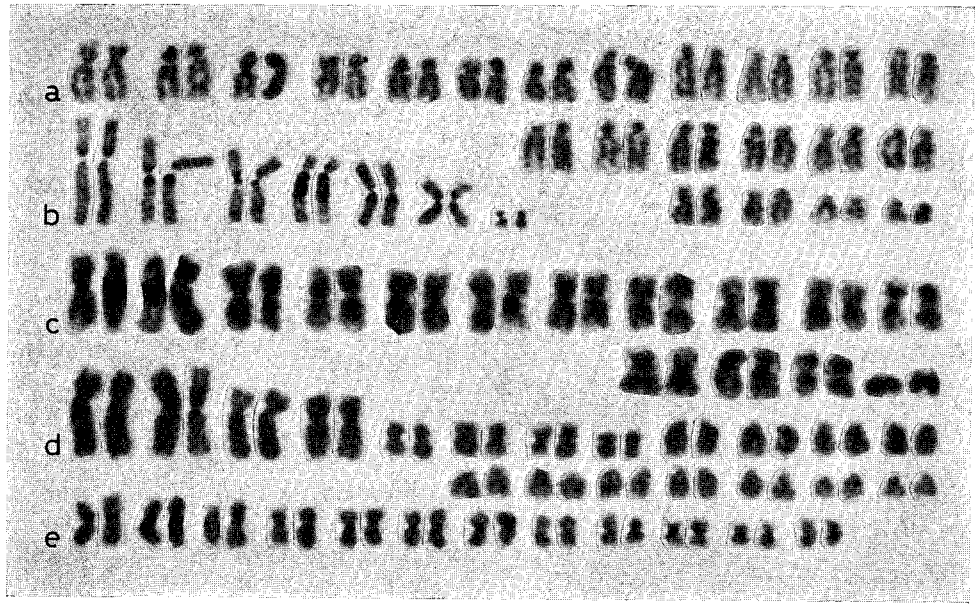

Fig. 4. Karyotypes of ponerine ants (IV) and a doryline ant (e). a. *Centromyrmex feae* (2*n*=44). b. *Diacamma vagans* (2*n*=14). c. *D. sp. 2* (2*n*=30). d. *Ectomomyrmex sp.* (2*n*=38). e. *Aenictus brevicornis* (2*n*=24).

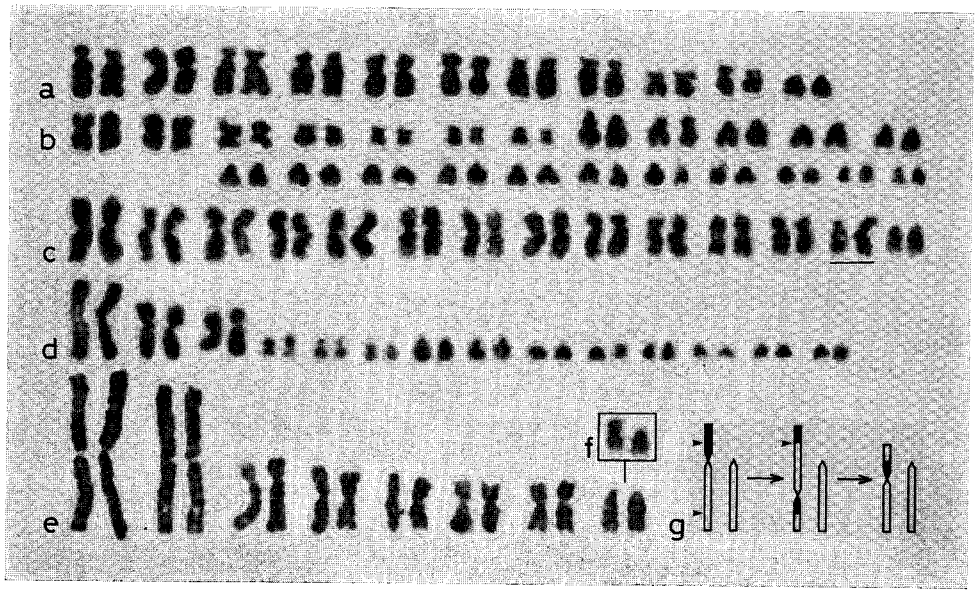

Fig. 5. Karyotypes of ponerine ants (V), a cerapachyne ant (c), and myrmicine ants (I). a. *Brachyponera luteipes* (2*n*=22). b. *Odontoponera transversa* (2*n*=46). c. *Cerapachys biroi* (2*n*=28). d. *Cardiocondyla nuda* (2*n*=28). e and f. *Meranoplus bicolor* (2*n*=16).

Diacamma: Three colonies of *D. vagans* (one from Calcutta and two from Mysore) were examined. The karyotype comprises 12 large $\bar{M}$ chromosomes and two minute $\bar{M}$'s ($2K=14\bar{M}$), of which the large members (especially No. 2 ST) are characterized by a well developed pericentromeric heterochromatin block (Fig. 4b). This peculiar karyotype composition was observed in all the colonies analyzed. Another species (denoted as *ps. 2*) found in Mysore showed, however, a quite different karyotype ($2K=2\bar{A}+28\bar{M}$, Fig. 4c) from that of *vagans*.

Ectomomyrmex: The karyotype of *E. sp.* found at Ranchi is represented in Fig. 4d, which consists of 8 extremely large $\bar{M}$ chromosomes and 30 small $\bar{M}$ or $\bar{A}$ chromosomes ($2K=22\bar{A}+16\bar{M}$).

Brachyponera (=*Pachycondyla*): *B. luteipes* (=*P. obscurans*, based on the suggestion by W. L. Brown, Jr.) was collected only in northern India (Chandigarh, Simla and New Delhi). Fig. 5a shows the karyotype of the colony from New Delhi, where $2K=2\bar{A}+20\bar{M}$.

Odontoponera: *O. transversa* found at Pinjore has a fairly high chromosome number ($2n=46$), and the diploid karyotype consists of $32\bar{A}$ and $14\bar{M}$ (Fig. 5b). The largest $\bar{A}$ chromosome pair has a large heterochromatin block at the proximal part of the long arm.

2) *Subfamily Cerapachyinae*

This group of ants is famous for massive predatory raids against other ants. Although about 200 species are known in the world, karyological survey has never been made, so that *Cerapachys biroi* examined here is the first karyological report for this family. Two colonies were collected from the botanical garden in Calcutta. The chromosome number was $2n=28$ in both colonies, which is a moderate number in Formicidae. The karyotype involves 12 pairs of $\bar{M}$ chromosomes, all of very similar size, one pair of slightly smaller $\bar{A}$ chromosomes, and one small pair is heteromorphic ($\bar{A}/\bar{M}$) probably due to constitutive heterochromatin polymorphism in short arms ($2K=3\bar{A}+25\bar{M}$, Fig. 5c).

3) *Subfamily Myrmicinae*

The Myrmicinae represent the biggest ant subfamily, and more than 3,000 species divided into some 130 genera have been recorded until now. In the present paper we report karyotypes of 45 species included in 15 genera.

Cardiocondyla: The chromosome number of *C. nuda* is $2n=28$, as was observed in a colony from Calcutta. The karyotype of this species ($2K=16\bar{A}$

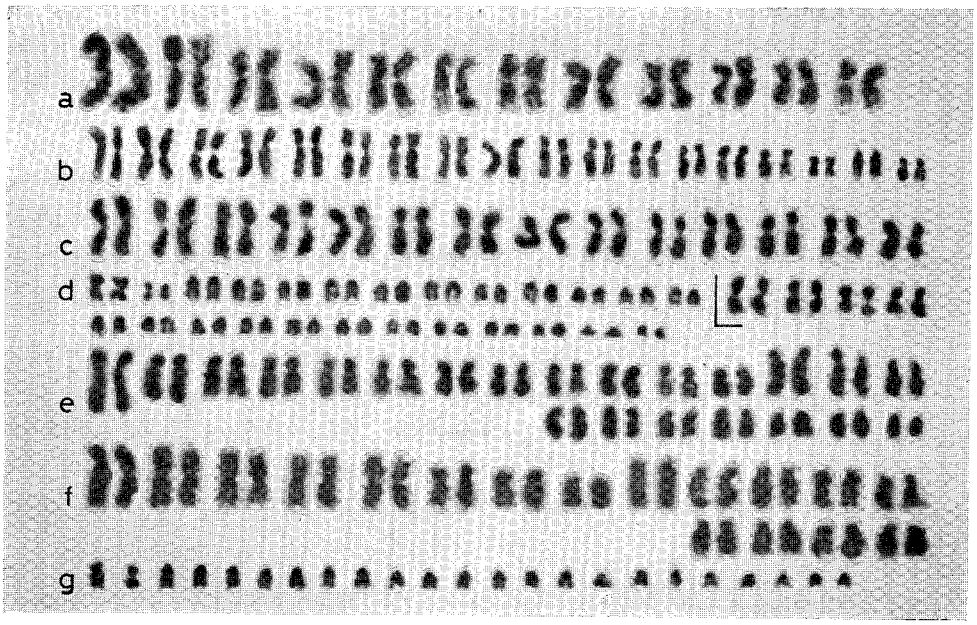

Fig. 6. Karyotypes of myrmicine ants (II). a. *Crematogaster biroi* ($2n=24$). b. *C. brunnea* ($2n=36$). c. *C. subnuda* ($2n=36$). d. *C. rothneyi* ($2n=50$). e. *Myrmicaria brunnea* ($2n=44$). f. *Aphaenogaster smythiesi* ($2n=34$). g. *A. beccarii* ($n=23$).

$+12\bar{M}$) is somewhat unusual, because it comprises three pairs of very large $\bar{M}$ chromosomes and 11 pairs of extremely small $\bar{M}$ or $\bar{A}$ chromosomes (Fig. 5d).

Meranoplus: *M. bicolor* was abundant in Chandigarh, New Delhi, Ranchi, and Calcutta. All the colonies examined showed $2n=16$, and the karyotype is characterized by 4 extremely large $\bar{M}$, 10 small $\bar{M}$'s, and two small $\bar{A}$'s ($2K=2\bar{A}+14\bar{M}$, Fig. 5e). A pericentric inversion polymorphism was found in one colony from Ranchi (HI78-99), in which the smallest chromosomes are heteromorphic ($\bar{A}/\bar{M}$) (Fig. 5f). The fact that the size of $\bar{M}$ is slightly larger than $\bar{A}$ may be due to insertion of a pericentromeric heterochromatin block by the process suggested in Fig. 5g.

Crematogaster: Four species were collected from Chandigarh, New Delhi, Ranchi, Calcutta, and Mahabaleshwara. The diploid karyotype of each species is formulated as $2K=24\bar{M}$ in *C. biroi* (Fig. 6a), $2K=4\bar{A}+32\bar{M}$ in *C. brunnea* (Fig. 6b), $2K=(0\text{-}5)\bar{A}+(31\text{-}36)\bar{M}$ in *C. subnuda* (Fig. 6c), and $2K=46\bar{A}+4\bar{M}$ in *C. rothneyi* (Fig. 6d). The karyotype of *C. biroi* is related to that of *C. rothneyi* mainly by Robertsonian rearrangements, because their arm numbers are fairly constant ($2AN=48$ and 54) in spite of great differences in chromosome number ($2n=24$ and 50). *C. brunnea* and *C. subnuda* are karyotypically

almost identical, though the $2AN$ values of the latter fluctuate slightly (68–70) by C-band polymorphism in short arms. Pericentric inversion and especially tandem growth of constitutive heterochromatin (t.g.c.h.) may predominate in these two species.

Myrmicaria: Two colonies of *M. brunnea* were collected in Ranchi, and their karyotypes were $2K=20\bar{A}+24\bar{M}$ (Fig. 6e). The same chromosome number ($2n=44$) was observed also in three Malaysian species of this genus (Goñi *et al.* 1982).

Aphaenogaster: The known chromosome numbers of this genus are $2n=20$, 22, 32, 34, and 40 (Crozier 1975), whereas Indian *Aphaenogaster* have rather higher numbers ($2n=34$ and 46). Two species, *A. smythiesi* (from Simla) and *A. beccarii* (from Mahabaleshwara), were examined. The former has $2K=18\bar{A}+16\bar{M}$ (Fig. 6f), and the latter is characterized by an acrocentric-rich karyotype, $2K=42\bar{A}+4\bar{M}$ (or $K=21\bar{A}+2\bar{M}$, Fig. 6g).

Pheidole: The genus *Pheidole* is one of the largest genera of myrmicines and is a taxonomically chaotic group. Indeed, among the 13 species studied here, 9 species could not be assigned to scientific names. These probably represent new species, at least in part. Their chromosome numbers are $2n=12$, 18, 28, 30 and 42. $2n=12$ of *P. mus* from Mahabaleshwara is the lowest record of this genus, and the karyotype comprises only $\bar{M}$ chromosomes ($2K=12\bar{M}$) (Fig. 7a). *P. woodmasoni* (found in Chandigarh and Simla) and *P. sp. 14* (Calcutta) have totally identical karyotypes ($2K=18\bar{M}$, Figs. 7b and 7c). The karyotypes of the members with $2n=20$ (*indica, rotschana, sp. 3, 4, 8, 9* and *11*) are formulated as $2K=20\bar{M}$, though the largest chromosome 1 is heteromorphic (Figs. 7d, 7e, 7f, 7g, 8a and 8b, see the underlined chromosomes). Chromosome 1 of *P. indica* is ST (Fig. 7d), and significantly larger than that of the remaining species. In *P. sp. 3* and *P. sp. 8*, one homolog of chromosome 1 has an elongate long arm, probably due to t.g.c.h. (Figs. 7e and 7g). Thus the arm ratio (r) is 2.0–2.1 in one of the two but 2.5–2.6 in the other. Such a heteromorphism was also observed in *P. sp. 4* (r=2.1 and 1.4; Fig. 7f) and in *P. sp. 11* (r=1.4 and 1.1, Fig. 8b). Since the chromosome size of these homologs is conserved in *P. sp. 4* and *P. sp. 11*, these cases may be interpreted by pericentric inversion polymorphism. Chromosome 1 of *P. sp. 9* (Fig. 8a) is very similar in shape and size to that of the species having $2n=18$. Although we failed to obtain good metaphase figures, *P. roschana* is karyotypically comparable to *P. sp. 9*. The four remaining species (*P. sp. 13*, *P. sp. 5*, *P. latinoda* and *P. sp. 1*) showed higher chromosome numbers than $2n=20$, and their karyotypes are formulated respectively as $2K=12\bar{A}+16\bar{M}$ (Fig. 8c), $2K=12\bar{A}+18\bar{M}$ (Fig. 8d), $2K=22\bar{A}+20\bar{M}$ (Fig. 8e) and $2K=22\bar{A}+20\bar{M}$ (Fig. 8f).

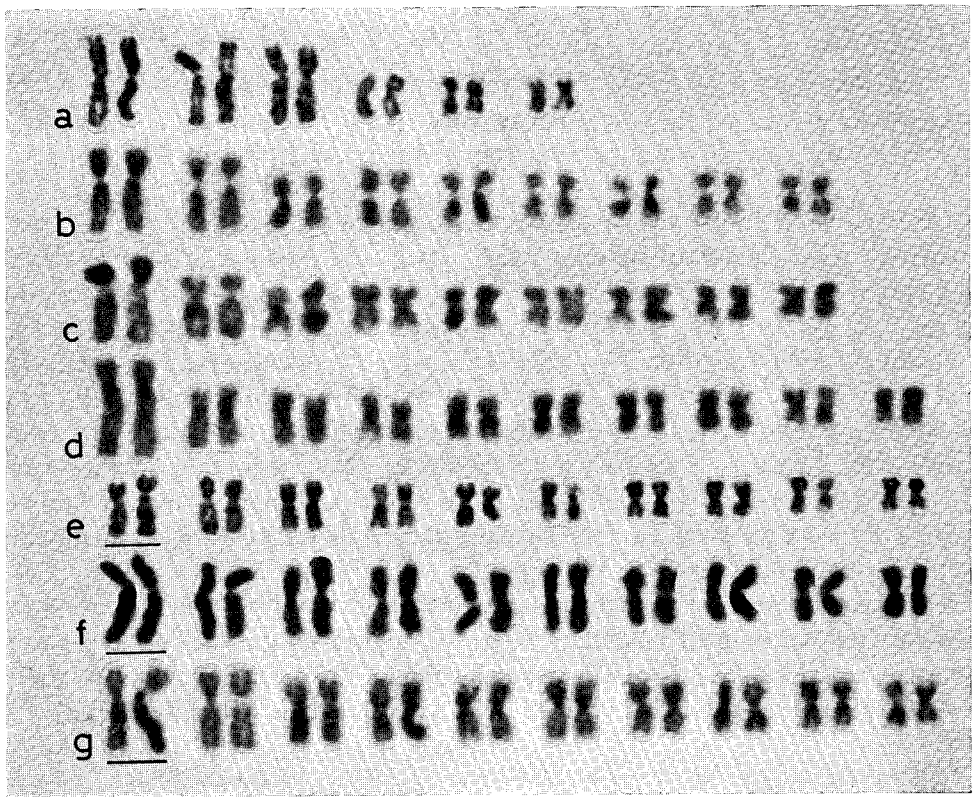

Fig. 7. Karyotypes of myrmicine ants (III). a. *Pheidole mus* (2*n*=12). b. *P. woodmasoni* (2*n*=18). c. *P. sp.14* (2*n*=18). d. *P. indica* (2*n*=20). e. *P. sp. 3* (2*n*=20). f. *P. sp. 4* (2*n*=20). g. *P. sp. 8* (2*n*=20).

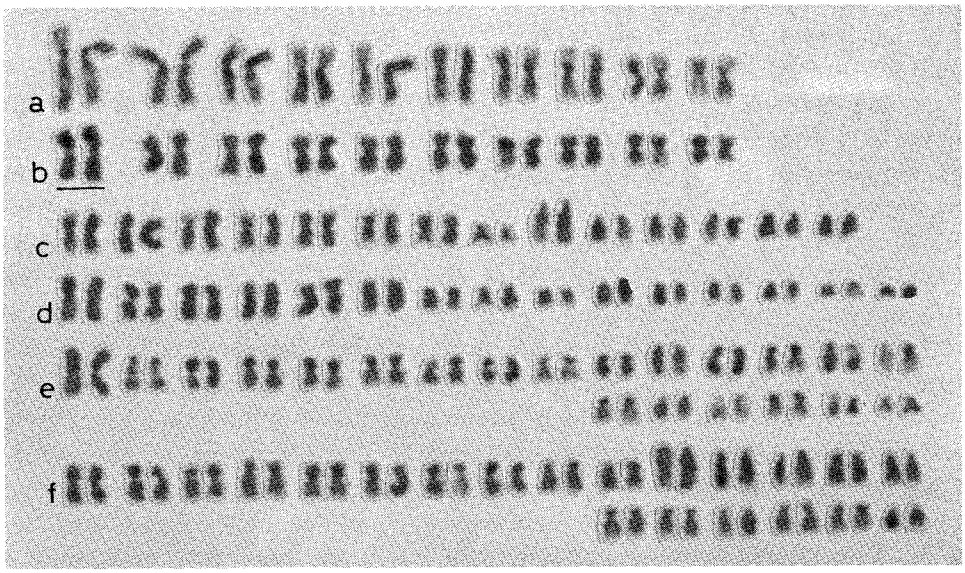

Fig. 8. Karyotypes of myrmicine ants (IV). a. *Pheidole sp. 9* (2*n*=20). b. *P. sp. 11* (2*n*=20). c. *P. sp. 13* (2*n*=28). d. *P. sp. 5* (2*n*=30). e. *P. latinoda* (2*n*=42). f. *P. sp. 1* (2*n*=42).

The last two species thus have identical karyotypes. In these species arm number increases with increasing chromosome number ($2AN=44$-62 and $2n=28$-42), suggesting that both Robertsonian rearrangement and pericentric inversion have played an important role in their karyotypic evolution.

Oligomyrmex: Four species examined have $2n=26$, 32, and 44. *O. sp. 5* collected from Calcutta had the lowest reported chromosome number in this genus ($2n=26$), and all chromosomes were metacentric ($2K=26\bar{M}$, Fig. 9a). *O. sp. 4* ($K=6\bar{A}+10\bar{M}$, Fig. 9b) was collected from Northern India (Dehra Dun and Ranchi). On the other hand, *O. asinus*, which was collected in Chandigarh and New Delhi, has $2K=36\bar{A}+8\bar{M}$ (Fig. 9c). These three species differ in chromosome number ($2n=26$, 32 and 44) but their arm number is the same ($2AN=52$), suggesting karyotype alteration by Robertsonian rearrangement. *O. sp. 2* ($2K=18\bar{A}+26\bar{M}$, Fig. 9d) has the same chromosome number with *O. asinus* ($2n=44$) but arm number is remarkably high ($2AN=70$), probably due to increase of short arm size by t.g.c.h.

This paper contains the first karyological information on three species representing three previously karyologically unknown genera. The species in question are *Pheidologeton diversus* ($2K=30\bar{A}+12\bar{M}$, Fig. 9e), *Lophomyrmex bedoti* ($2K=28\bar{A}+10\bar{M}$, Fig. 9g), and *Trigonogaster sp.* ($2K=6\bar{A}+18\bar{M}$, Fig. 9f).

Monomorium: The known chromosome number of this genus is $2n=22$, 34 and 42 (Crozier 1975; Imai *et al.* 1977, 1983), in which 8 of 10 species karyotyped have $2n=22$. Our present investigation revealed, however, that the chromosome number of *Monomorium* ranges between $2n=16$-70. The lowest number ($2n=16$) was observed in *M. dichroum*, where $2K=16\bar{M}$, and two of them are extremely large in size (Fig. 10a). *M. orientale* with $2n=20$ also shows only $\bar{M}$ chromosomes ($2K=20\bar{M}$, Fig. 10b). At least two Robertsonian rearrangements and 4 pericentric inversions may be needed for interpreting the karyotype differentiation of these two species. The karyotypes of the species with $2n>22$ are summarized as follows: *M. sp. 5* $2K=14\bar{A}+20\bar{M}$ (Fig. 10c), *M. glabrum* $2K=10\bar{A}+28\bar{M}$ (Fig. 10e), *M. sp. 6* $2K=8\bar{A}+30\bar{M}$ (Fig. 10f), and *M. latinode* $2K=60\bar{A}+10\bar{M}$ (Fig. 10g). Note that in these species, as well as in *Pheidole* mentioned above, arm number increases with increasing chromosome number ($2AN=32$-80 and $2n=16$-70). The chromosome number $2n=70$ found in *M. latinode*, which was collected from Mahabaleshwara, is the second highest number in the present report. The karyotype of this species is characterized by a high number of acrocentrics. An unique translocation polymorphism was found in *M. indicum* collected from Chandigarh and New Delhi. Details will be discussed later, but we stress here that two types of colonies, with $2n=22$ and 21, were observed, and that those individuals with

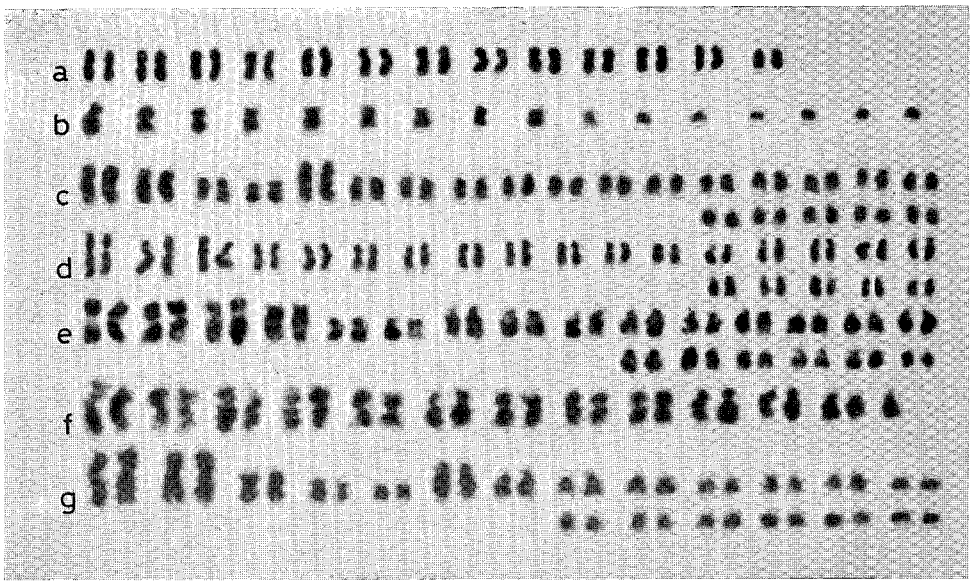

Fig. 9. Karyotypes of myrmicine ants (V). a. *Oligomyrmex sp. 5* ($2n=26$). b. *O. sp. 4* ($n=16$). c. *O. asinus* ($2n=44$). d. *O. sp. 2* ($2n=44$). e. *Pheidologeton diversus* ($2n=42$). f. *Trigonogaster sp.* ($2n=24$). g. *Lophomyrmex bedoti* ($2n=38$).

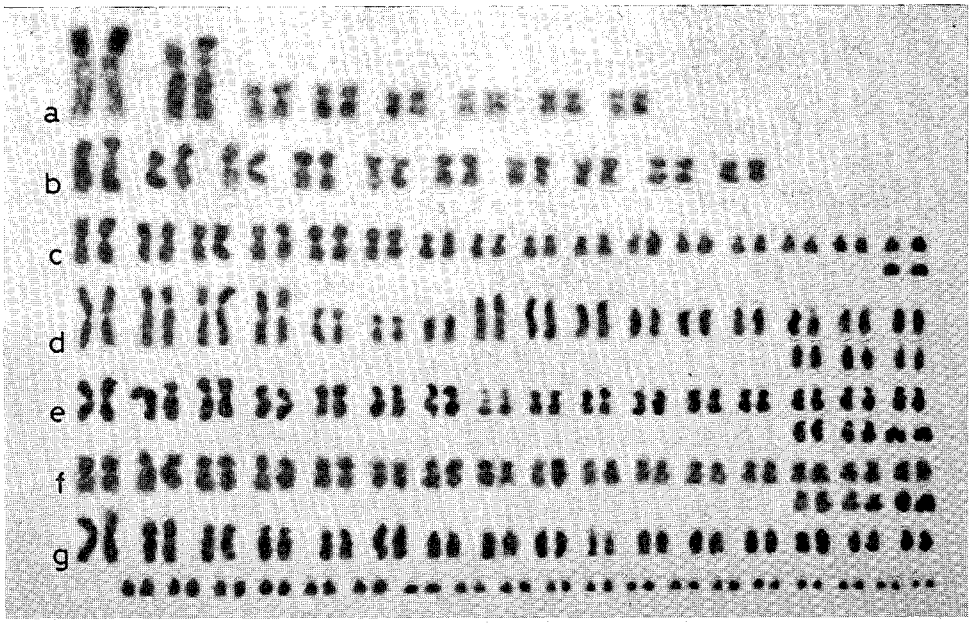

Fig. 10. Karyotypes of myrmicine ants (VI). a. *Monomorium dichroum* ($2n=16$). b. *M. orientale* ($2n=20$). c. *M. sp. 5* ($2n=34$). d. *M. scabriceps* ($2n=38$). e. *M. glabrum* ($2n=38$). f. *M. sp. 6* ($2n=38$). g. *M. latinode* ($2n=70$).

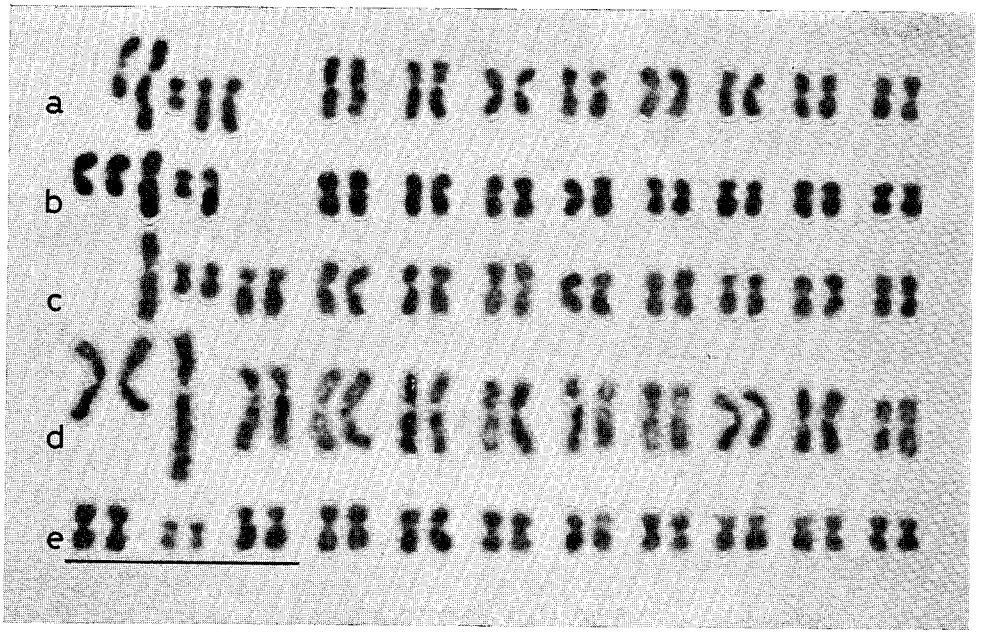

Fig. 11. A reciprocal translocation polymorphism found in *Monomorium indicum*. a and d. $2n=21$ (HI78-55). b and c. $2n=21$ (HI78-56). e. $2n=22$ (HI78-25). For details see Fig. 20a.

$2n=22$ have homomorphic karyotype ($2K=20\bar{M}$, Fig. 11e) while those with $2n=21$ are chromosomally highly heterogeneous (Figs. 11a-d and 20a).

Messor: One colony of *Messor sp.* (a new species) was collected at Chandigarh. This is the southernmost record for the genus in Asia. The diploid karyotype consisted of $34\bar{A}$ and $7\bar{M}$ (Fig. 12a). The odd chromosome number $2n=41$ has resulted from Robertsonian polymorphism in chromosome 1 (see the underlined chromosomes in the figure).

Solenopsis: Five colonies of *S. geminata* were collected from Ranchi, Calcutta, Poona, and Mysore. This species is generally known as the fire ant and is undergoing range expansion in many parts of the world. The chromosome number was $2n=32$ in all these colonies, representing what is supported to be the natural range of the species, though arm number varies between $2AN=58$-62, probably caused by C-band polymorphism in short arms. One karyotype with $2AN=58$ (i.e., $2K=6\bar{A}+26\bar{M}$) is demonstrated in Fig. 12b. The karyotype of this species was already reported by Crozier (1970a) who, from a colony of probable North American origin, obtained $2n=32$ and $2AN=46$. These observations suggest that arm number fluctuates not only geographically but even intercolonially in this species.

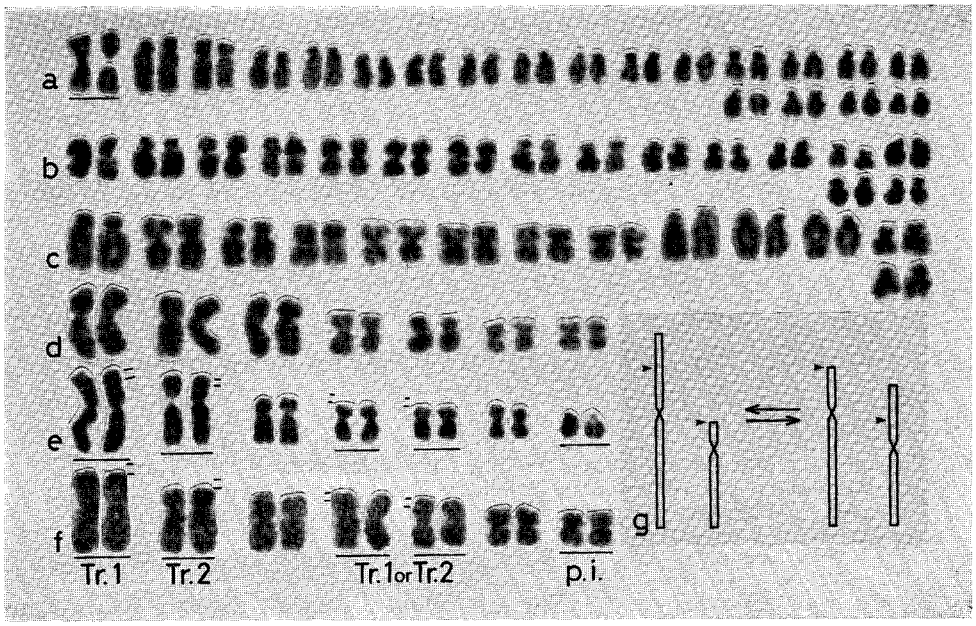

Fig. 12. Karyotypes of myrmicine ants (VII). a. *Messor sp.* ($2n=41$). Chromosome 1 underlined is heteromorphic ($\bar{M}/2\bar{A}$) due to Robertsonian polymorphism. b. *Solenopsis geminata* ($2n=32$). c. *Tetramorium smithi* ($2n=26$). d. *T. simillimum* ($2n=14$). e. *Triglyphothrix lanuginosa* ($2n=14$). f. *T. walshi* ($2n=14$). g. A scheme of reciprocal translocation found in the karyotypes between *T. lanuginosa* and *T. walshi*. Chromosomes and chromosome segments contributed are represented by underlines and small double bars.

Tetramorium: Three species were examined. *T. simillimum* collected from Chandigarh and Ranchi had the same karyotype $2K=14\bar{M}$ (Fig. 12d). A somewhat higher number ($2n=26$) was observed in *T. smithi* from Ranchi in which the diploid karyotype is $2K=10\bar{A}+16\bar{M}$ (Fig. 12c). A complicated chromosome polymorphism was found in *T. sp. 3* collected from Mahabaleshwara. Three colonies examined showed an odd chromosome number $2n=35$, and the diploid karyotype composed of 12 pairs of $\bar{A}$ chromosomes and 3 pairs of $\bar{M}$ chromosomes. The remaining chromosomes ($3\bar{M}$ and $2\bar{A}$) were, however, unpaired (Figs. 13b and c). One cell with a minute chromosome (m) and thus $2n=36$ was observed in the colony HI78-163 (Fig. 13a). The detailed karyotype analysis suggested that this chromosome polymorphism was produced by two centric fissions, one centric fusion, and elimination of a minute chromosome (m) (Fig. 13d).

Triglyphothrix: Two species examined showed the same chromosome number $2n=14$. *T. lanuginosa* may be distributed widely in India, because two colonies were collected from Chandigarh and one from Mysore. The

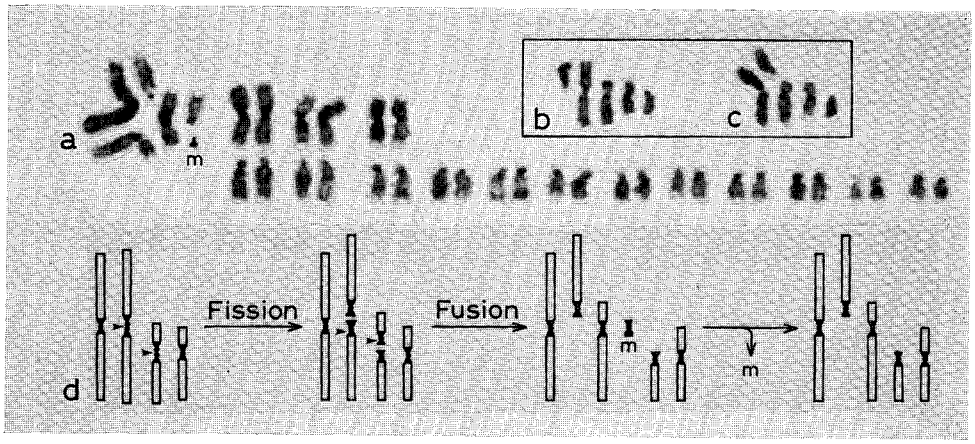

Fig. 13. Polymorphic karyotypes of *Tetramorium sp. 3*. a. A cell with a minute (m; $2n=36$). b and c. Two cells without the minute ($2n=35$). d. A scheme of karyotype alteration in *T. sp. 3*, in which two centric fissions, one centric fusion and deletion of minute (m) are assumed.

karyotype was $2K=2\bar{A}+12\bar{M}$ (Fig. 12e). On the other hand, *T. walshi* was found only in northern India (Chandigarh, New Delhi and Ranchi) and has a slightly different karyotype from *T. lanuginosa*, $2K=14\bar{M}$ (Fig. 12f). The karyotype of *T. walshi* may have been produced from that of *T. lanuginosa* by one pericentric inversion in the smallest chromosome and two reciprocal translocations, as suggested in Fig. 12g, or vice versa. We suggested that one translocation, denoted as Tr. 1 occurred between chromosome 1 and 4 or 5, and the other (Tr. 2) between chromosome 2 and 4 or 5 (see short double bars in Figs. 12e and f).

4) *Subfamily Dorylinae*

This ant group is known as army ants, because of well developed nomadic movements for predatory raids. Karyological reports for this subfamily are scarce. The only published record involves *Aenictus sp.* (near *camposi*) from Taiwan, studied by Hung *et al.* (1972), in which chromosome number was $2n=30$. We examined here another *Aenictus* species, *A. brevicornis*, which was collected in Chandigarh. As is shown in Fig. 4e, the karyotype involves $22\bar{M}$ chromosomes and two acrocentrics ($2K=2\bar{A}+22\bar{M}$).

5) *Subfamily Dolichoderinae*

The members of this subfamily tend to have lower chromosome numbers than others, i.e., most of the species observed show $2n=10$-18, and a few $2n=22$, 28, and 32 (Crozier 1975; Imai *et al.* 1977). This tendency was also observed in the present study. We examined five species involved in three genera and obtained $2n=10$, 10, 16, 18, and 28.

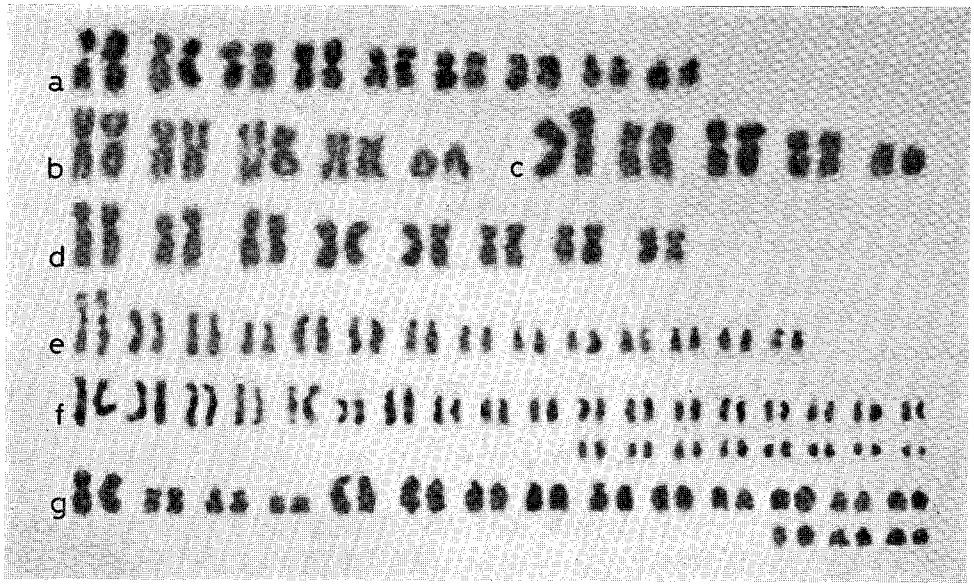

Fig. 14. Karyotypes of dolichoderine ants (a–e) and formicine ants (I). a. *Iridomyrmex anceps* ($2n=18$). b. *Tapinoma melanocephalum* ($2n=10$). c. *T. indicum* ($2n=10$). d. *Technomyrmex albipes* ($2n=16$). e. *T. sp. 2* ($2n=28$). f. *Cataglyphis setipes* ($2n=54$). g. *Anoplolepis longipes* ($2n=34$).

Iridomyrmex: One colony of *I. anceps* was collected from Ranchi. The karyotype was $2K=4\bar{A}+14\bar{M}$ (Fig. 14a).

Tapinoma: Two species, *T. melanocephalum* and *T. indicum*, were examined. The former was collected from Mysore, and the latter from Chandigarh, New Delhi, and Mahabaleshwara. These two species showed completely identical karyotypes $2K=2\bar{A}+8\bar{M}$ (Figs. 14b and 14c).

Technomyrmex: *T. albipes* is found in India and Australia. Indian *albipes* collected from Dehra Dun have $2K=16\bar{M}$ (Fig. 14d). This karyotype is identical to that of Australian material of this species from Leumeah, N.S.W. (Imai *et al.* 1977). Crozier (1968) obtained somewhat different results, i.e., he observed $2n=18$ in a colony of *T. albipes* from Sandringham (Victoria). The *albipes* with $2n=18$ has two extremely small SM and A chromosomes, which correspond to the long and short arm of the smallest metacentric (chromosome 8) of Indian *albipes*, respectively. The karyotype with $2n=18$ may be derived from that with $2n=16$ by one centric fission and one pericentric inversion, though we need further investigations to determine whether the individuals with $2n=18$ are polymorphic or sibling species. *T. sp. 2* collected from Chandigarh is closely related to *T. bicolor* in morphology and has $2K=20\bar{A}+8\bar{M}$ (Fig. 14e).

6) *Subfamily Formicinae*

Formicinae is the second largest ant subfamily, in which about 1,500 species (44 genera) have been recorded. In the present study, we examined 23 species included in 7 genera. Formicine ants of India are characterized by highly divergent chromosome numbers, i.e., $2n=16$, 18, 20, 24, 26, 28, 30, 34, 35, 39, 40, 42, 44, and 54. Three types of chromosome polymorphism (C-band, fission-inversion, and Robertsonian) were found in *Camponotus*.

Cataglyphis: One species, *C. setipes*, collected from Chandigarh, had an acrocentric-rich karyotype $2K=40\bar{A}+12\bar{M}$ (Fig. 14f). Almost the same chromosome number ($n=26$) was observed by Hausteck-Jungen in *C. albicans* and *C. bicolor* (Crozier 1975).

Acantholepis: Four species of *Acantholepis* (*lunaris*, *sp. 1*, *capensis*, and *sp. 2*) were collected in the areas of Chandigarh, Ranchi and Poona. All of them show completely identical karyotypes $2K=2\bar{A}+16\bar{M}$ (Fig. 15).

Anoplolepis: Three colonies of *A. longipes* were collected from Poona and Mysore, and they were karyotypically homomorphic, $2K=26\bar{A}+8\bar{M}$ (Fig. 14g). The same chromosome number ($2n=34$) was observed also in a Malaysian species (Goñi *et al.* 1983).

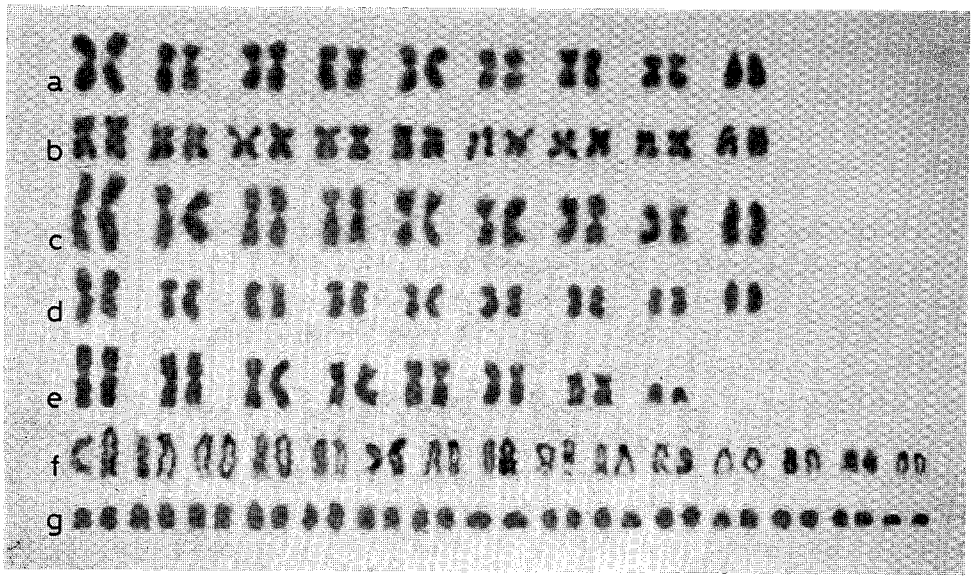

Fig. 15. Karyotypes of formicine ants (II). a. *Acantholepis capensis* ($2n=18$). b. *A. lunaris* ($2n=18$). c. *A. sp. 1* ($2n=18$). d. *A. sp. 2* ($2n=18$). e. *Paratrechina longicornis* ($2n=16$). f. *P. sp. 3* ($2n=30$). g. *P. indica* ($2n=30$).

Paratrechina: Three species, *P. longicornis*, *P. sp. 3*, and *P. indica* were examined. *P. longicornis* is widely distributed in India. All the six colonies collected from Chandigarh, New Delhi, Ranchi, Poona, and Mahabaleshwara showed $2K=2\bar{A}+14\bar{M}$ (Fig. 15e). This species, widespread in the world tropics through human activities, has been karyotypically studied also in Taiwan (Hung *et al.*, 1972). No chromosome difference has been found between the Indian and Taiwan material of this species. Another two species (*P. sp. 3* and *P. indica*) found in Calcutta and Dehra Dun are characterized by an acrocentric-rich karyotype, $2K=30\bar{A}$ in the former (Fig. 15f) and $2K=28\bar{A}+2\bar{M}$ in the latter (Fig. 15g). As the arm number of these three species is fairly constant ($2AN=30$ or 32) in spite of a remarkable difference in chromosome number ($2n=16$-30), Robertsonian rearrangement may be important for their karyotype alteration.

Oecophylla: Three colonies of *O. smaragdina* collected from Ranchi, Calcutta and Poona showed the same karyotype $2K=16\bar{M}$ (Fig. 16a). Our results are comparable with those on Malaysian *smaragdina* reported by Crozier (1970).

Camponotus: This genus is one of the largest among the ants, more than 1,000 species having been recorded in the world, and the taxonomy of the

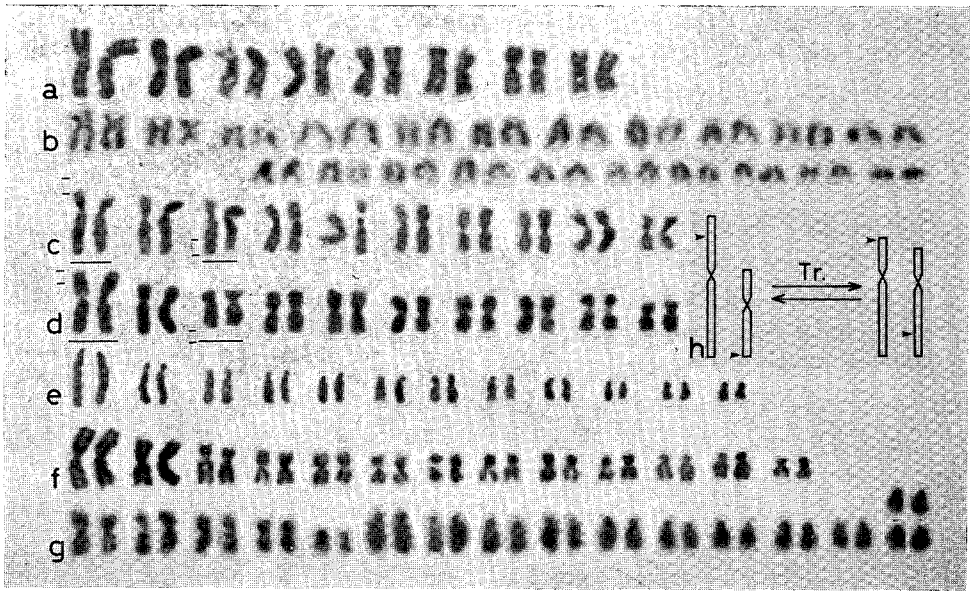

Fig. 16. Karyotypes of formicine ants (III). a. *Oecophylla smaragdina* ($2n=16$). b. *Polyrhachis simplex* ($2n=42$). c. *Camponotus dolendus* ($2n=20$). d. *C. mitis* ($2n=20$). e. *C. taylori* ($2n=24$). f. *C. variegatus* ($2n=26$). g. *C. sp. 7* ($2n=32$). h. A scheme of reciprocal translocation found in *C. dolendus* and *C. mitis* (see underlines and small double bars).

group is confused. We examined 12 Indian *Camponotus* species, four of which could not be assigned scientific names. This ant genus is as karyotypically heterogeneous as its species are morphologically divergent. The known chromosome numbers range between $2n=18$ and 50 (Crozier 1975). Rather divergent chromosome numbers were also found among Indian *Camponotus*. We observed $2n=20$, 24, 26, 32, 34, 35, 39, 40, and 44. Three species, *C. dolendus*, *C. mitis*, and *C. sp. 10*, have the lowest number ($2n=20$) among Indian representatives. The karyotypes of these species are formulated $2K=20\bar{M}$, though chromosomes 1 and 3 are morphologically different between *C. dolendus* and the other. In the *C. dolendus*, chromosomes 1 and 3 are ST, and their size is almost comparable with that of chromosome 2 (Fig. 16c). On the other hand, these pairs are SM or M in the other two species. Note that chromosome 1 is slightly larger than chromosome 3 in *mitis* (Fig. 16d) and *sp. 10*. The karyotype of *sp. 10*, not illustrated here, is identical to that of *mitis*. The karyotypic differences of these three species may be interpreted simply by assuming that one reciprocal translocation occurred between chromosomes 1 and 3. A possible scheme of the chromosome rearrangement involved is represented in Fig. 16h. *C. taylori* collected from Calcutta are not very different in chromosome number ($2n=24$) from *C. dolendus* or *C. mitis*, but they are karyotypically quite different: all chromosomes are acrocentric in *C. taylori* ($2K=24\bar{A}$, Fig. 16e). Four species of the *C. variegatus* group were collected from Chandigarh, Poona, and Mahabaleshwara, of which two colonies, HI78-152 and 171, were identified as genuine *variegatus*. The karyotype of HI78-171 is $2K=6\bar{A}+20\bar{M}$ (Fig. 16f), while $2K=26\bar{M}$ is shown by HI78-152. The karyological difference between these two colonies is probably due to C-band polymorphism in the short arms, rather than to pericentric inversion polymorphism. Three colonies, HI78-38, 157, and 26 are karyotypically closely related to *C. variegatus*, although each appears to represent a morphologically distinct species, tentatively named *C. sp. 7*, *C. sp. 12*, and *C. sp. 9*, respectively. The first two species have slightly different karyotypes: $2K=22\bar{A}+10\bar{M}$ in *sp. 7* (Fig. 16g) and $2K=24\bar{A}+10\bar{M}$ in *sp. 12* (Fig. 17a). Two chromosomally different individuals were observed in *C. sp. 9* (collected from Chandigarh), one of which had $2n=34$ and the other $2n=35$. The difference in chromosome number has resulted from fission-inversion polymorphism (Fig. 18). Details will be discussed later (Fig. 20b). Three further species of *Camponotus*, *C. crassisquamis*, *C. paria* and *C. thraso*, have identical karyotypes, $2K=40\bar{A}$ (Figs. 17b, 17d and 17e), though a few chromosomes of *C. paria* have small heteromorphic short arms. Robertsonian polymorphism was found in the colony of *C. crassisquamis* collected from Ranchi, in which $2K=39\bar{A}+1\bar{M}$ (Fig. 17c). *C. sericeus* obtained in Ranchi showed $2K=42\bar{A}+2\bar{M}$ (Fig. 17f). Note that the chromosome number of Indian *Camponotus* varies widely between $2n=20$ and 44, while their arm number ranges around $2AN=40$, ex-

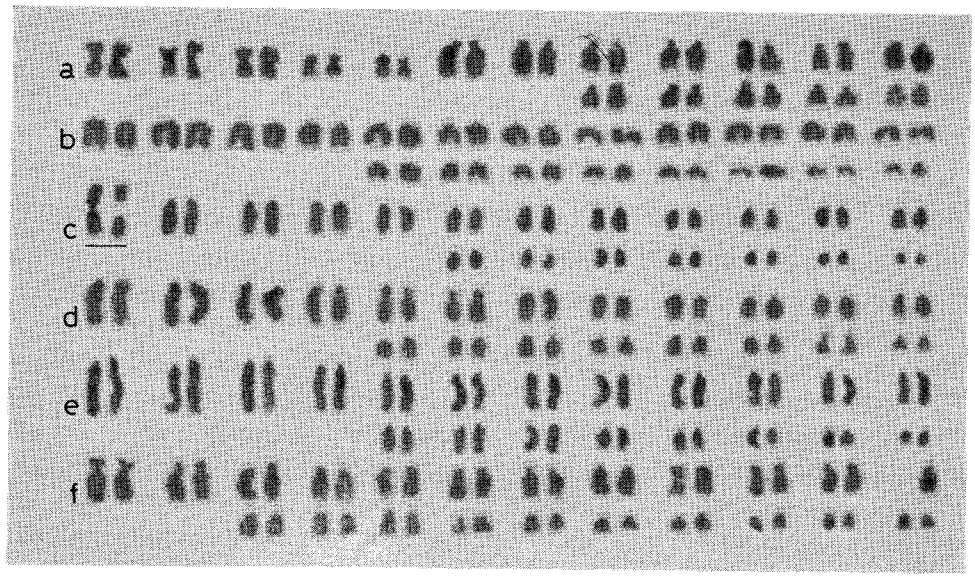

Fig. 17. Karyotypes of formicine ants (IV). a. *Camponotus sp. 12* ($2n=34$). b. *C. crassisquamis* ($2n=40$). c. *C. crassisquamis* ($2n=39$). Chromosome 1 (underlined) is heteromorphic ($\bar{M}/2\bar{A}$) by Robertsonian polymorphism. d. *C. paria* ($2n=40$). e. *C. thraso* ($2n=40$). f. *C. sericeus* ($2n=44$).

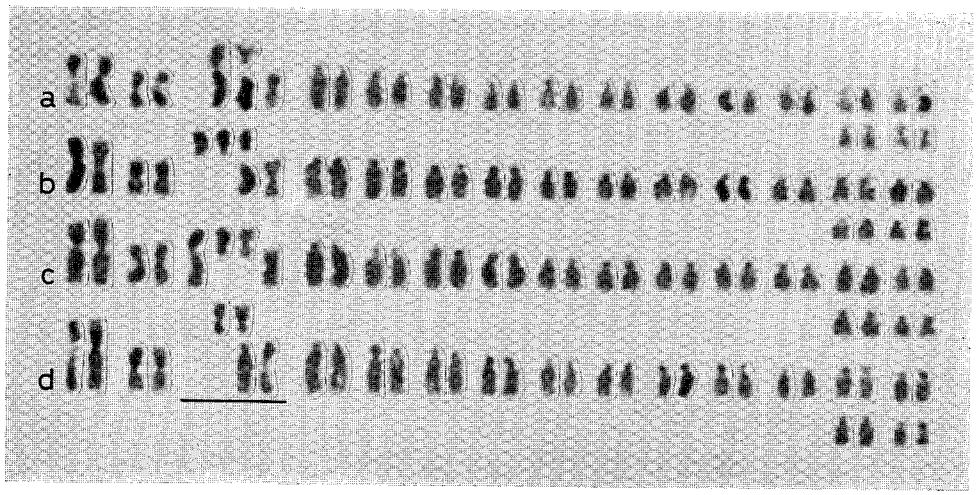

Fig. 18. Karyotypes of *Camponotus sp. 9* with fission-inversion polymorphism. a, c, and d $2n=34$. b. $2n=35$. The marker chromosomes are underlined. For details see Fig. 20b.

cepting *C. taylori* ($2AN=24$), suggesting karyotype alteration by Robertsonian rearrangement.

Polyrhachis: One colony of *P. simplex* was found in Chandigarh. The karyotype was $2K=36\bar{A}+6\bar{M}$ (Fig. 16b).

4. DISCUSSION

Although the number of species sampled is not yet sufficient for a quantitative analysis of karyotype evolution in ants, the frequency distribution of chromosome number is obviously bimodal with an antimode at $n=11$ (Fig. 19). Based on this antimode, we classify Indian ants into two groups; lower-numbered species having $n\leq 11$, and higher-numbered species ($n>11$). This dichotomy seems to be a real feature of karyotype evolution in ants, because an almost identical distribution pattern was found in Australian ants (Imai *et al.* 1977). Comparison of the two curves by the Kolmogorov-Smirnov test permitted us confidently to reject the hypothesis that they are different ($D=.2239$, $p\gg.2$). Interestingly, hymenopterans other than ants are characterized mostly by the lower number ($n\leq 11$) (Crozier 1975; Naito 1982), though we need further accumulation of karyological data before conclution.

The two groups mentioned above seem to be quite opposite in the mode of karyotype alteration. The karyotypes of the ants with low chromosome numbers are composed mainly of $\bar{M}$ chromosomes, and chromosome size distribution is remarkably variable among different lineages in spite of conservatism in chromosome number (e.g., compare Figs. 4b, 5e, 7a, 12e, and 14d). The same phenomenon was observed in hymenopterans other than ants (Naito 1978a,b). Since most of the $\bar{M}$ chromosomes have euchromatic arms, and since constitutive heterochromatin is rather rarely found (Fig. 4b), reciprocal translocation (though it has generally been considered to be a rare rearrangement in animal

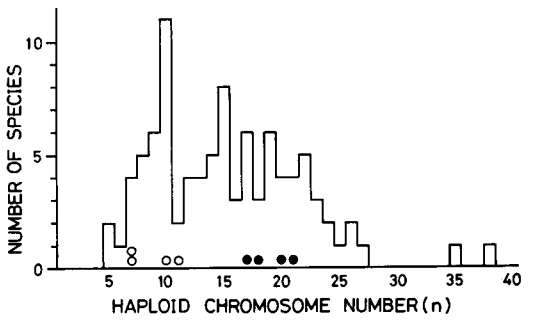

Fig. 19. Frequency distribution of chromosome numbers in Indian ants. Open circles: karyotypes with translocation polymorphism or translocations fixed. Solid circles: karyotypes with Robertsonian polymorphisms.

karyotype evolution) may be the only available rearrangement for producing size variation of chromosomes in the lower-numbered species. Indeed, we found one reciprocal translocation polymorphism in *Monomorium indicum* (Fig. 11), and at least three translocations may have contributed to the karyotype differentiation between *Camponotus dolendus* (Fig. 16c) and *C. mitis* (Fig. 16d), and between *Triglyphothrix lanuginosa* (Fig. 12e) and *T. walshi* (Fig. 12f).

In contrast, $\bar{A}$ chromosomes are abundant in the higher-numbered species, in which chromosome number varies widely, but their karyotype alterations are interpreted (without translocations) as the combination of Robertsonian rearrangement, pericentric inversion, and tandem growth of constitutive heterochromatin (t.g.c.h.) in short arms. We found four Robertsonian polymorphism: *Messor sp.* (Fig. 12a), *Tetramorium sp. 3* (Fig. 13), *Camponotus sp. 9* (Fig. 18), and *C. crassisquamis* (Fig. 17b and 17c). Arm number variation by t.g.c.h. was found in *Crematogaster subnuda* (Fig. 6c), *Solenopsis geminata* (Fig. 12b), and *Camponotus variegatus* (Fig. 16f).

Imai *et al.* (1977) suggested that pericentric inversions have played an important role in karyotype alteration in both the lower- and higher-numbered species. In the present paper, we found one pericentric inversion polymorphism in a lower-numbered species (*Meranoplus bicolor*; Figs. 5e and 5f), and another example was obtained in a higher-numbered species (*Camponotus sp. 9*; Fig. 18). Pericentric inversions detected as polymorphism are very few in the present paper, but we suggested in the previous section that a number of pericentric inversions, as well as Robertsonian rearrangements, would have been fixed during the karyotype evolution of ants.

Nonrandom distribution of Robertsonian and translocation polymorphisms was pointed out first in Australian ants by Imai *et al.* (1977). Our present data indicate that the phenomenon also applies in the Indian ants (Fig. 19). For example, translocations were found only in the lower-numbered species, while Robertsonian rearrangements appeared only in the higher-numbered species. Because of significant reduction of fertility in heterozygotes, it is theoretically expected that translocation would seldom have contributed to karyotype evolution (e.g., Wright 1941; Bengtsson and Bodmer 1976), and this expectation has been confirmed in many animal groups (White 1973). In ants, however, gametic and zygotic selection in heterozygotes with chromosome aberrations may be less deleterious. As suggested in Fig. 20, individuals bearing partial monosomy, trisomy, and even tetrasomy which have resulted from non-disjunction, seem to be viable and probably fertile. This may explain the frequent appearance of translocation polymorphisms in ants. The nonrandom distribution of Robertsonian and reciprocal translocation polymorphisms in ants was interpreted by Imai *et al.* (1977) as follows: "translocations arise at a constant, although low, rate in all lineages, but that, in those lineages

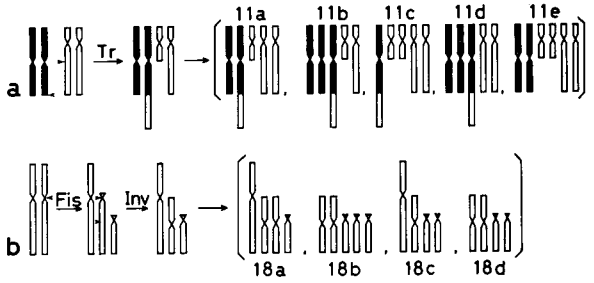

Fig. 20. Schematic representations of chromosome alterations found in *Monomorium indicum* (a) and *Camponotus sp. 9* (b). Tr: reciprocal translocation. Arrow heads: breakage points assumed. Fiss: centric fission. Inv: pericentric inversion. Individuals segregated from translocation or fission-fusion heterozygotes by non-disjunction are represented in parentheses. Note that monosomic, trisomic, and tetrasomic individuals are viable and probably fertile in ants. Karyotypes of each example are demonstrated in Figs. 11a–e and 18a–d.

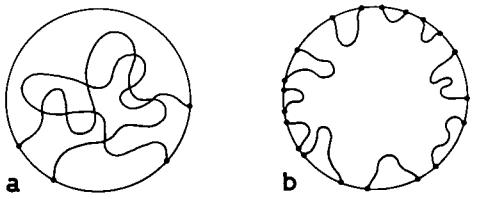

Fig. 21. Comparison of chromosome configurations in interphase nuclei between an hypothetical karyotype with large sized (and thus low numbered) chromosomes (a) and that having small sized (i.e., high numbered) chromosomes (b). Note that if the genome size is equal between the two karyotypes and if the terminals of bivalents are attached to the nuclear membrane, the bivalents will interact more frequently in the former (a) than in the latter (b). Solid circles: terminals attached to the nuclear membrane known as the basal knob (Solari 1970) or the terminal attachment plaque (Moses 1977).

undergoing rapid numerical change, subsequent Robertsonian change (fission) soon eliminates any evidence in the form of contributed observable heterozygosity for translocation. In slowly-changing lineages, however, the evidence of translocation will persist longer". This interpretation assumes *a priori* that breakage and reunion resulting in translocation is a totally random event, so that if it occurs nonrandomly an alternative interpretation is required. Recent advances in cytogenetics have shown that both terminals of bivalents are attached to the nuclear membrane at pachytene; these terminals are usually denoted as the basal knob (Solari 1970) or the terminal attachment plaque (Moses 1977). This pattern indicates a nonrandom configuration of interphase chromosomes. It is a theoretically reasonable assumption that chromosome rearrangements occurring in germ cells can primarily contribute to karyotype evolution. Therefore, if reciprocal translocations occur at pachy-

tene by an abnormality of the crossing-over mechanism, such rearrangements will appear less frequently in karyotype having higher-numbered (and thus small-sized) chromosomes, because effective chromosome interaction would be reduced importantly by fixing chromosome terminals on the nuclear membrane (Fig. 21). This problem was attacked by a Monte Carlo simulation method, the results of which will be published elsewhere by Imai, Maruyama, and Crozier. This alternative hypothesis, though we need further accumulation of cytological evidence, suggests an answer to a basic question: if the fission hypothesis proposed by Imai *et al.* (1977) in ants and Imai and Crozier (1980) in mammals is correct, why are chromosome numbers apt to increase? The answer is "to reduce the genetic load due to translocation".

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