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THE CHROMOSOME OBSERVATION TECHNIQUES OF ANTS AND THE CHROMOSOMES OF FORMICINAE AND MYRMICINAE

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Introduction

There are only a few studies on the chromosomes of ants. Whelden and Haskins (1953) studied with 19 varied species, and they reported that the haploid chromosome number was constant at n=5 in all these species. Besides this, there have been some other reports on a few genera, i.e., *Camponotus* (Lams, 1908), *Formica* (Schleip, 1908), *Lasius* (Henking, 1892; Hogben, 1920), and *Oecophylla* (Ledoux, 1954). But these studies were mostly concerned with embryogeny, spermatogenesis or oogenesis. From these results it is not possible to decide the correct chromosome number of these species, because the chromosomes of ants are very small, and the descriptions are open to question.

In recent years, Peacock et al. (1954) succeeded in observing the chromosome number of *Monomorium pharaonis*, and excellent studies were made by Hauschteck (1961, 1962). She reported on 18 species in two subfamilies, Formicinae and Myrmicinae (listed in Table 1).

The present author has also succeeded in obtaining suitable chromosome preparations and photographs from ant material, upon which a report has been made (Imai, 1965) on the chromosome numbers of 22 Japanese species in 4 subfamilies (Ponerinae, Dolichoderinae, Myrmicinae, and Formicinae). The present paper reports on some chromosome observation techniques and provides more detailed chromosome observations on Japanese Myrmicinae and Formicinae. Since some interesting

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characters of the chromosome complement appeared in these two subfamilies, some phylogenetic considerations are discussed on the basis of the data of Hauschteck (1962) and Peacock et al. (1954) in combination with counts from 19 Japanese species.

Materials and Methods

1. Biological note

The materials mainly used are the pupae of males and queens prepared immediately after pupation. In the male pupae the color of the eyes turns into *slight rouge* in this stage, and the testes contain many haploid mitotic figures which are assumed to correspond to those of the first maturation division of a normal meiosis. In the case of the queen the *scarlet* eye stage is the most suitable, for at this time the queen ovary contains many diploid oogonial cell-divisions and the chromosome size is very large. The suitable stages are cited in Fig. 1.

The season during which these reproductive larvae appear is very limited. Therefore in many species the brain cells (cerebral ganglion) of worker ants were used; these showed a diploid number. In this case it is best to use the prepupal stage at which the head and neck region of the larva becomes transparent. Mitotic cell divisions also become active in this stage. In order to obtain the materials more surely a diploid or haploid parthenogenesis by workers is advantageous in some species, i.e., *Formica, Aphaenogaster, Messor, Pristomyrmex.* The eggs laid by workers generally develop into haploid males, and in some species also parthenogeneticaly into diploid workers or queens. Certainly these parthenogenetic larvae have exactly the same chromosome number as normal natural larvae, e.g., *Formica japonica, Polyergus samurai*, etc. The utilization of parthenogenetic larvae should be tested widely; it may become a most useful method for the study of ant chromosomes, because the parthenogenesis can be controlled by special breeding conditions. With *Formica*

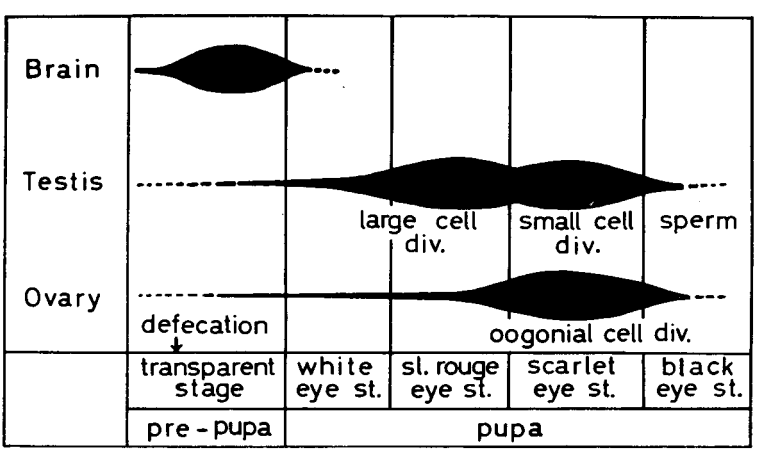
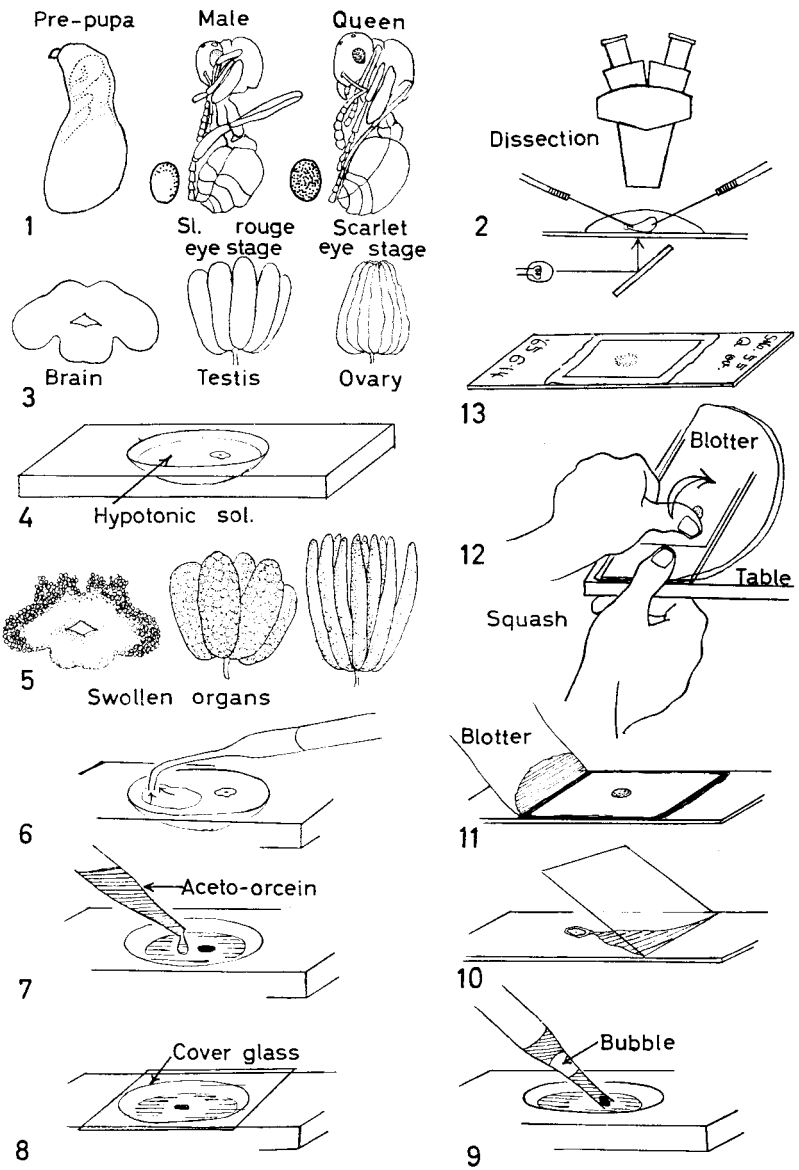


Fig. 1. Relation between pupal stage and relative frequency of mitotic figures containing in each organ, brain, testis, and ovary.



Hyaluronidase-aceto-orcein squash method

japonica, for example, the larvae can be produced all year round by breeding adult workers under special conditions.

2. Chromosome preparation

In the early work, the preparations were made by the usual simple aceto-orcein squash method. The mitotic figures were not spread well, and the chromosomes were all piled up, especially those species having large numbers, i.e., *Formica yessensis* (Plate 4; 16Q).

Recently the author has been able to observe very fine chromosomes by using the new improved methods described below. Especially the drying method is suitable for large-numbered species, because metaphase is spread several times better than by the squash method, and this makes it possible to see very fine chromosomes and to count the correct chromosome number easily.

(a) *Hyaluronidase-aceto-orcein squash method*

Each organ is removed from the pupae or prepupae of suitable stage by dissecting in Carlson's physiological salt solution for grasshoppers (Carlson, 1946). Preparations are generally made by the 1 % aceto-orcein (dissolved in 50 % glacial acetic acid) squash method (Fig. 2) after keeping them for ten minutes in a hypotonic solution consisting of 0.5 % sodium citrate solution 1 ml and hyaluronidase (for injection, 200 T. R. U. ampoule) 0.1 ml.

This method gives favourable preparations for the species having small chromosome numbers, i.e., *Pheidole*, *Monomorium*, *Aphaenogaster*, *Crematogaster*, etc. But it is less satisfactory for the species having more than forty or fifty chromosomes.

(b) *Drying method*

The drying method for mammalian tissues (Saksela and Morehead, 1962) was applied to overcome these difficulties. Preparation by this method was modified to the following procedure.

Testes or ovaries are gathered from ten or more reproductive pupae, cut into

Fig. 2. 1. Suitable observation stages. Transparent stage, pre-pupa (all castes); slight rouge eye stage for testis (male); scarlet eye stage for ovary (female). 2. Pupae are dissected in Carlson's solution under a binocular by using dissecting needles. 3. Removed organs are freed of tracheae, thin membrane, and fat-bodies, and placed in 4. 4. Hypotonic solution containing hyaluronidase fills depression slide and is incubated without moving for 10 min. at about 30–35°C. 5. Swollen organs. 6. Hypotonic solution is removed by micropipette with bent tip. 7. Aceto-orcein (1 %) fixative is added to half the depth of the depression. 8. A cover glass is positioned to prevent the evaporation of fixative, which is kept still for 30 min. incubating at about 30–35°C. 9. Each organ is removed with a small amount of aceto-orcein. It must be noticed that if the organ is sucked into pipette directly, the organ is apt to stick to the glass of the pipette and can not be removed easily. But this trouble can be prevented by first sucking a small bubble up into the pipette as illustrated in the figure. 10. The organ is dropped with fixative on the pre-cleaned glass slide and the slide inclined slightly to separate the organ and aceto-orcein so as to adhere the organ on the glass slide. 11. The excessive fixative is removed by a blotter. 12. Squashing. 13. A squash preparation is sealed with balsam-paraffin by spatula.

minute bits in Carlson's solution, and kept in the same hypotonic solution mentioned above (plus 0.2 ml 5 mg/ml trypsin dissolved in Carlson's solution) while incubating at 37°C for ten minutes. After this the preparation is mixed gently with a pipette to suspend the cells. The suspended isolated cells are fixed by addition of 0.5 ml of freshly mixed, chilled fixative (methyl alcohol 3 : glacial acetic acid 1). The cells are left undisturbed in this iced fixative for 30 minutes and then are resuspended by pipetting and centrifuged at about 1,000 r.p.m. for 3 minutes. The supernatant is discarded, 2 ml fixative newly added and the cells are again centrifuged in the same way. After two or three runs of this treatment, 0.1-0.2 ml fixative is finally added to make more condensed cell suspension. The suspension is dropped by a syringe on the wet surface of a pre-cleaned glass slide which previously has been dipped into 50% ethyl alcohol. Immediately the slide is dried by touching it on a flame to burn the alcohol. The slide is stained with lactic-orcein (lactic acid 170 ml, glacial acetic acid 130 ml, orcein 3 g) for two or twelve hours at 37°C, and after passing up through the concentration series of alcohol, the slides are covered.

By this method very excellent mitotic figures can be obtained in such as genera *Formica, Lasius* and *Tetramorium*, and it is even possible to analyse the karyotypes. It has the disadvantage that it does not work well with small-sized ants, because this method needs large amounts of mitotic cells.

Observed Results

(a) The list of chromosome numbers of Japanese Formicinae and Myrmicinae.

Chromosomes of a total of 19 Japanese ants were observed, 10 of the species are in Myrmicinae and 9 in Formicinae. The results for each species will be summarized briefly, and chromosome complements are figured.

Subfamily **Myrmicinae**

1. *Pheidole fervida*

The haploid chromosome number observed in male testes is 10. All 8 observed cells showed the same number n=10. The diploid chromosome number observed in the queen ovary is 20 (2 cells observed). The reproductive larvae were collected at Tokyo, June 1963. (Plate 1; 1M, 1Q). (The letters, M, Q, and W, are the abbreviations of male, queen, and worker, respectively).

2. *Monomorium pharaonis*

n=11 (♂, testes, 16 cells counted). Collected at Manazuru, Kanagawa prefect., June 1964. (Plate 1; 2M). This species is the same one observed by Peacock et al. (1954) and my sample shows the same chromosome number.

3. *Pristomyrmex pungens*

n=12 (♂, testes, 5 cells), 2n=24 (☿, brain, 3 cells). Collected at Manazuru, June 1963. (Plate 1; 3M, 3W). In this species no queens have been observed by me, and it has been said that workers lay diploid parthenogenetic eggs (Teranishi, 1929). The males originated from the haploid parthenogenetic eggs by workers were collected by chance this time.

4. *Leptothorax spinosior*

2n=24 (☿, brains, 7 cells). Collected at Mishima, Shizuoka prefect., June 1964. (Plate 1; 4W).

5. *Crematogaster laboriosa*

2n=26 (☿, brains, 21 cells). Collected at Shuzenji, Shizuoka prefect., June 1964. (Plate 1; 5W).

6. *Tetramorium caespitum*

n=14 (♂, testes, 11 cells), 2n=28 (Q, ovaries, 36 cells). Collected at Sugadaira, Nagano prefect., June 1963, and in 1964. (Plate 2; 6M, 6Q). The chromosome number of this species agrees with the count given by Hauschteck (1961).

7. *Aphaenogaster famelica*

n=17 (♂, testes, 14 cells), 2n=34 (Q, ovaries and brains, 21 cells). Collected at Tanzawa, Kanagawa prefect., June 1963, and in 1965. (Plate 2; 7M, 7Q).

8. *Aphaenogaster* sp.

n=16 (♂, testes and brains, 79 cells), 2n=32 (Q, ovaries and brains, 9 cells). Collected at Manazuru, June 1964, and in 1965. (Plate 2; 8M). This species seems to be the same one described by Teranishi (1940), as *Aphaenogaster famelica* var. *osimensis*. Dr. Brown advised the present author in his personal communication that this species should have been separated from *A. famelica* at species level.

9. *Vollenhovia emeryi*

n=18 (♂, testes, 9 cells), 2n=36 ☿, brains, 12 cells). Collected at Kawazu, Shizuoka prefect., July 1965. (Plate 3; 9W).

10. *Messor aciculatum*

n=22 (♂, testes, 15 cells), 2n=44 (Q, ovaries, 8 cells). Collected at Mishima, July 1964, and observed in November 1964, using pupae developed from impaternate worker eggs. (Plate 3; 10M, 10Q).

Subfamily **Formicinae**

11. *Camponotus* sp.

n=9 (♂, testes, 5 cells), 2n=18 (Q, ovaries and brains, 150 cells). Collected at Manazuru, June 1964. (Plate 3; 11M, 11Q). This species is called "Nawayotsuboshi-ooari" in Japan, but the appropriate scientific name is not available at present. It is, however, clear that this species differs from other *Camponotus* groups in chromosome number.

12. *Camponotus kiusiuensis*

2n=28 (☿, brains, 7 cells). Collected at Odawara, July 1964. (Plate 3; 12W).

13. *Camponotus japonicus*

n=14 (♂, testes, 13 cells). Collected at Sugadaira, July 1963. (Plate 3; 13M). Male pupae devloped from haploid parthenogenetic workers were used.

14. *Lasius niger*

2n=30 (Q, ovaries, 37 cells). Collected at Shuzenji, May 1964. (Plate 4; 14Q). The chromosome number of this species agrees with the count given by Hauschteck (1961).

15. *Lasius talpa*

2n=30 (Q, ovaries, 9 cells). Collected at Sugadaira, June 1963. (Plate 4; 15

Q).

16. *Formica yessensis*

n=26 (♂, testes, 35 cells), 2n=52 (Q, ovaries, 10 cells.). Collected at Sugadaira, July 1963, and in 1964. (Plate 4; 16M, 16Q).

17. *Formica sanguinea*

n=26 (♂, testes, 37 cells), 2n=52 (Q, ovaries, 11 cells). Collected at Sugadaira, July 1964. (Plate 5; 17M, 17Q).

18. *Formica japonica*

n=27 (♂, testes, 243 cells), 2n=54 (Q, ovaries, 8 cells). Collected at Tokyo, June 1962, 1963, 1964, and in 1965. (Plate 5; 18M, 18Q). Haploid parthenogenesis of workers produced the male pupae.

19. *Polyergus samurai*

n=27 (♂, testes, 11 cells), 2n=54 (Q, ovaries, 3 cells). Collected at Tokyo, June 1963. (Plate 4; 19M). Suitable photographs of diploid chromosome figures could not be taken, but sketches were drawn.

(b) Chromosome numbers in Myrmicinae and Formicinae.

The total number of species in which chromosome number has been properly observed in these two subfamilies is 35. The known counts are summarized as follows.

1. Myrmicinae: Observations have been made on 18 species. The haploid chromosome number ranges n=4, 9, 10, 11, 12, 13, 14, 16, 17, 18, 22. Thus, variation of number is very wide in this subfamily, and the haploid number series is virtually continuous (Fig. 3 upper). These numbers clearly show a heteroploid relationship. Among this series, the species with n=11, 12, 14 are the most abundant.

2. Formicinae: Observations have been made on 18 species. The haploid number falls into three groups: the first group shows n=8, 9 in *Prenolepis* and *Camponotus* respectively. The second group shows n=14, 15. To this group belong most species of *Camponotus* and *Lasius*. The third group has rather large numbers n=26, 27 and includes all species of *Formica* and *Polyergus* so far checked (Fig. 3 lower). The number relations among these three groups may indicate slight devi-

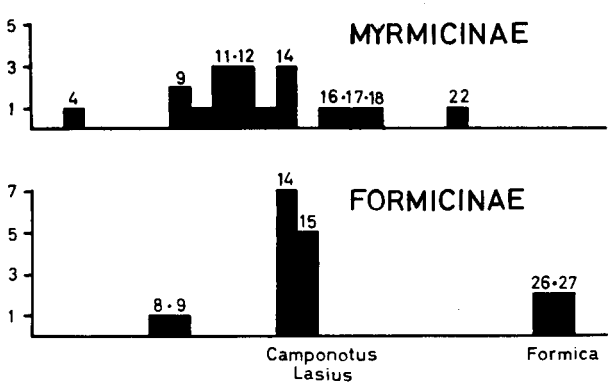


Fig. 3. A comparison of haploid numbers in subfamilies Myrmicinae and Formicinae.

ation from euploid multiples. (It is interesting to note that the haploid number 5, believed by Whelden and Haskins, 1953, to be basic in Formicidae, has not yet been found by any later worker in any ant species.)

Table 1. Chromosome numbers Myrmicinae and Formicinae.

Subfamily Myrmicinae

		n	2n
1.	*Stenamma brevicorne*		8
2.	*Leptothorax tuberum nigriceps*		18
3.	*Leptothorax tuberum tuberum*		18
4.	*Pheidole fervida*	10	20
5.	*Aphaenogaster subterranea*		22
6.	*Solenopsis fugax*	11	22
7.	*Monomorium pharaonis*	11	22
8.	*Leptothorax spinosior*		24
9.	*Pheidole pallidula*		24
10.	*Pristomyrmex pungens*	12	24
11.	*Crematogaster laboriosa*		26
12.	*Strongylognathus huberi alpina*		28
13.	*Tetramorium caespitum*	14	28
14.	*Aphaenogaster* sp.	16	32
15.	*Aphaenogaster famelica*	17	34
16.	*Vollenhovia emeryi*	18	36
17.	*Messor aciculatum*	22	44

Subfamily Formicinae

		n	2n
18.	*Prenolepis imparis*		16
19.	*Camponotus* sp.	9	18
20.	*Camponotus kiusiuensis*		28
21.	*Camponotus japonicus*	14	
22.	*Camponotus lateralis*		28
23.	*Camponotus vagus*	14	28
24.	*Camponotus ligniperda*	14	28
25.	*Lasius fuliginosus*		28
26.	*Lasius alienus*		28
27.	*Lasius emarginatus*		30
28.	*Lasius umbratus*		30
29.	*Lasius flavus*		30
30.	*Lasius niger*		30
31.	*Lasius talpa*		30
32.	*Formica sanguinea*	26	52
33.	*Formica yessensis*	26	52
34.	*Formica japonica*	27	54
35.	*Polyergus samurai*	27	54

Discussion

Hauschteck (1962) considered that Formicinae had generally larger chromosome numbers than Myrmicinae, as based on species of *Lasius* and *Camponotus* compared with the myrmicid genus *Pheidole* and other species. However, as described above, the Myrmicinae contain many species having relatively large chromosome numbers, i.e., *Vollenhovia* n=18, *Messor* n=22, while in *Myrmica rubra* the haploid number n=23, 24, 26 was observed, although further investigation must be made on this last species in order to decide the correct number. On the other hand, in Formicinae there also can be found large-numbered groups, such as *Formica* n=26 and 27, and *Polyergus* n=27. On the basis of these pitifully few counts, we may speculate as follows.

Both subfamilies show very wide variation in chromosome numbers, but the tendency of number-grouping differs. The chromosome number of genera of Myrmicinae shows continuous series of variation. From this variation of number, as a whole, we may consider the possibility of a heteroploid relationship like that well known in many plants. On the other hand, in Formicinae the haploid numbers tend to gather into three distinct groups. The relationship among these three groups may perhaps be considered as showing a polyploid relationship. Moreover it may be a very interesting common character in both of these subfamilies that some of those genera having rather large chromosome numbers, e.g., *Formica*, *Myrmica*, and *Messor* live in rather high latitudes or in arid areas, recalling the opinions of Suomalainen (1950) and Stebbins (1950) concerning polyploid species and their distribution. These authors thought that polyploid animals and plants may possess ability superior to simple diploids in adapting to harsh environments and newly-opened regions. If it is considered that these two subfamilies have been evolving along independent lines, the fundamental difference in the pattern of number variation which appears in these subfamilies so far is very interesting and suggestive.

Brown (1954) expressed his opinion on the subfamilies of Formicidae; on a primarily morphological basis he divided the Formicidae into two main lineages; the Poneroid Complex, including Myrmicinae, and the Myrmecioid Complex, including Formicinae. It is sufficient to suggest that these morphologically very different groups may also show some karyological differences along the lines summarized.

Another interesting difference of both subfamilies is the variation tendency of chromosome numbers among related species or genera. Myrmicinae not only contains many kind of genera and shows very wide variation of chromosome number among genera (Fig. 3 upper) but it also includes many species which show number variations among related species in the same genus, e.g., in *Pheidole*, *Aphaenogaster*, and *Leptothorax*. Moreover, these species often show different chromosome numbers between Japanese and European species, even when they belong the same genus (see Table 1). In Formicinae there are fewer genera than in Myrmicinae, and the variation within one genus tends to be very narrow, e.g., in *Camponotus*, *Lasius*, and *Formica*. In these genera there are no differences in chromosome number between European and Japanese species.

Is this wide variation tendency characteristic only of Formicinae and Myrmicinae in Formicidae? The author has some knowledge of other subfamily, Ponerinae, pos-

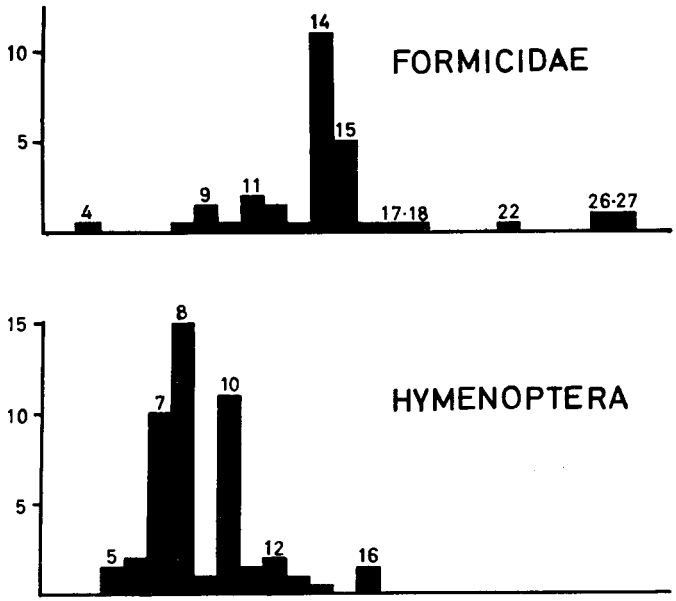


Fig. 4. A comparison of haploid numbers of Formicidae and of other Hymenoptera (Hymenoptera data from White, 1954).

sibly a primitive group. I observed in two ponerine species, *Brachyponera luteipes* n=11, 2n=22; and *Cryptopone sauteri* 2n=28 (Imai, 1965). Beside this *Ponera* or *Hypoponera* sp. was counted at n=5, 6, 7, although further observation must be done to decide the correct number. Another knowledge was given by Mr. Crozier in his personal communication that recently he found some species having rather larger chromosome number. From these it is indicated that Ponerinae may also show a wide variation in chromosome number. Therefore, these wide-variation tendencies perhaps may be the general rule in Formicidae.

According to White (1954), most groups of Hymenoptera have haploid numbers ranging from 5 to 16, with modal number near n=7, 8, 10 (Fig. 4 lower). On the other hand Formicidae has haploid number n=4 to 27 (Fig. 4 upper). This result shows clearly that within the order, Formicidae have rather high counts on the average. Therefore we can conclude that the family Formicidae holds a very peculiar evolutionary position among the Hymenoptera from the karyological point of view. The evidence is, however, still too incomplete to give us any firm conclusions.

Summary

1. Chromosome observations on 19 Japanese ants, including Myrmicinae and Formicinae, were made with the help of the new hyaluronidase-aceto-orcein squash method and the drying method; good photographs of all species were obtained.

2. In chromosome numbers, it becomes clear that the Myrmicinae genera show a very wide heteroploid relationship, but Formicinae shows a nearly polyploid relationship, as based on haploid chromosome numbers that range n=4, 9, 10, 11, 12, 13, 14, 16, 17, 18, 22 in Myrmicinae and n=8, 9 : 14, 15 : 26, 27 in Formicinae.
3. Number variation among related species is wide in Myrmicinae, but narrow in Formicinae.
4. A wide variety of chromosome numbers is characteristic of Formicidae among Hymenoptera.

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Explanation of Plates

Plate 1

Fig. 1. *Pheidole fervida* 1M (♂, testis) n=10 ; 1Q (queen, ovary) 2n=20.
Fig. 2. *Monomorium pharaonis* 2M (♂, testis) n=11.
Fig. 3. *Pristomyrmex pungens* 3M (♂, testis) n=12 ; 3W (☿, brain) 2n=24.
Fig. 4. *Leptothorax spinosior* 4W (☿, brain) 2n=24.
Fig. 5. *Crematogaster laboriosa* 5W (☿, brain) 2n=26.

Plate 2

Fig. 6. *Tetramorium caespitum* 6M (♂, testis) n=14 ; 6Q (queen, ovary) 2n=28.
Fig. 7. *Aphaenogaster famelica* 7M (♂, testis) n=17 ; 7Q (queen, ovary) 2n=34.
Fig. 8. *Aphaenogaster* sp. 8M (♂, testis) n=16.

Plate 3

Fig. 9. *Vollenhovia emeryi* 9W (☿, brain) 2n=36.
Fig. 10. *Messor aciculatum* 10M (♂, testis) n=22 ; 10Q (queen, ovary) 2n=44.
Fig. 11. *Camponotus* sp. 11M (♂, testis) n=9 ; 11Q (queen, ovary) 2n=18.

Fig. 12. *Camponotus kiusiuensis* 12W (☿, brain) 2n=28.
Fig. 13. *Camponotus japonicus* 13M (♂, testis) n=14.

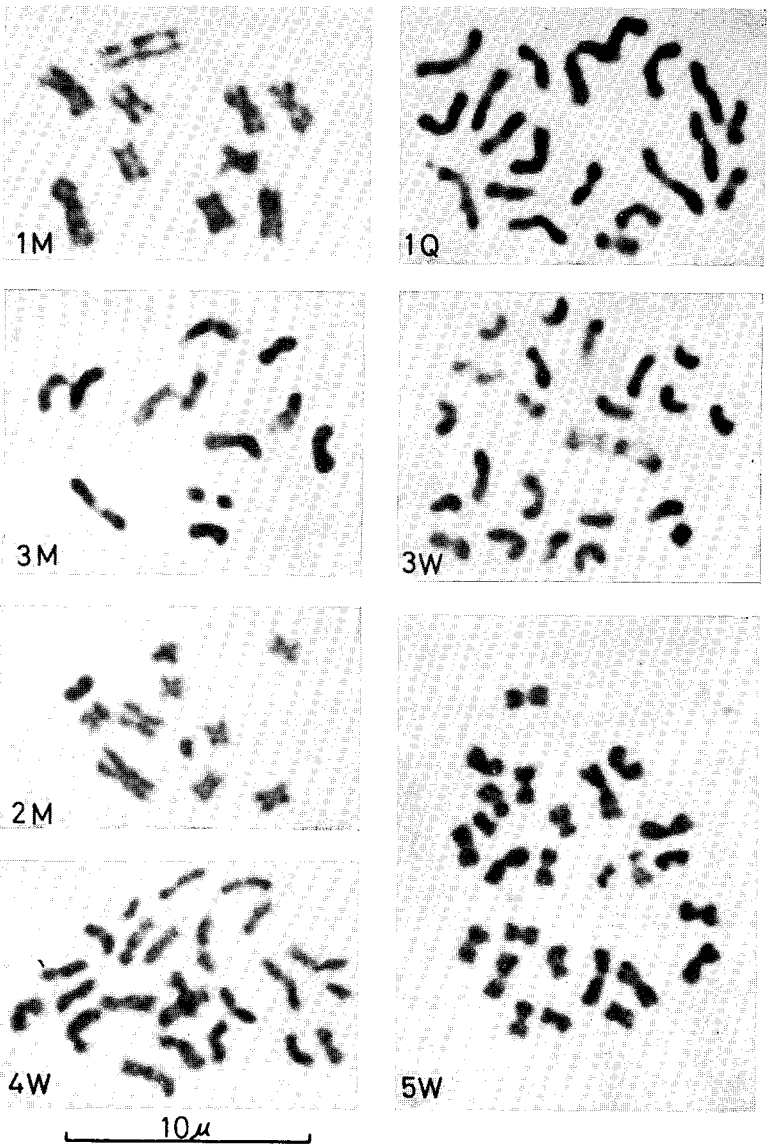
Plate 4

Fig. 14. *Lasius niger* 14Q (queen, ovary) 2n=30.
Fig. 15. *Lasius talpa* 15Q (queen, ovary) 2n=30.
Fig. 16. *Formica yessensis* 16M (♂, testis) n=26; 16Q (queen, ovary) 2n=52.
Fig. 19. *Polyergus samurai* 19M (♂, testis) n=27.

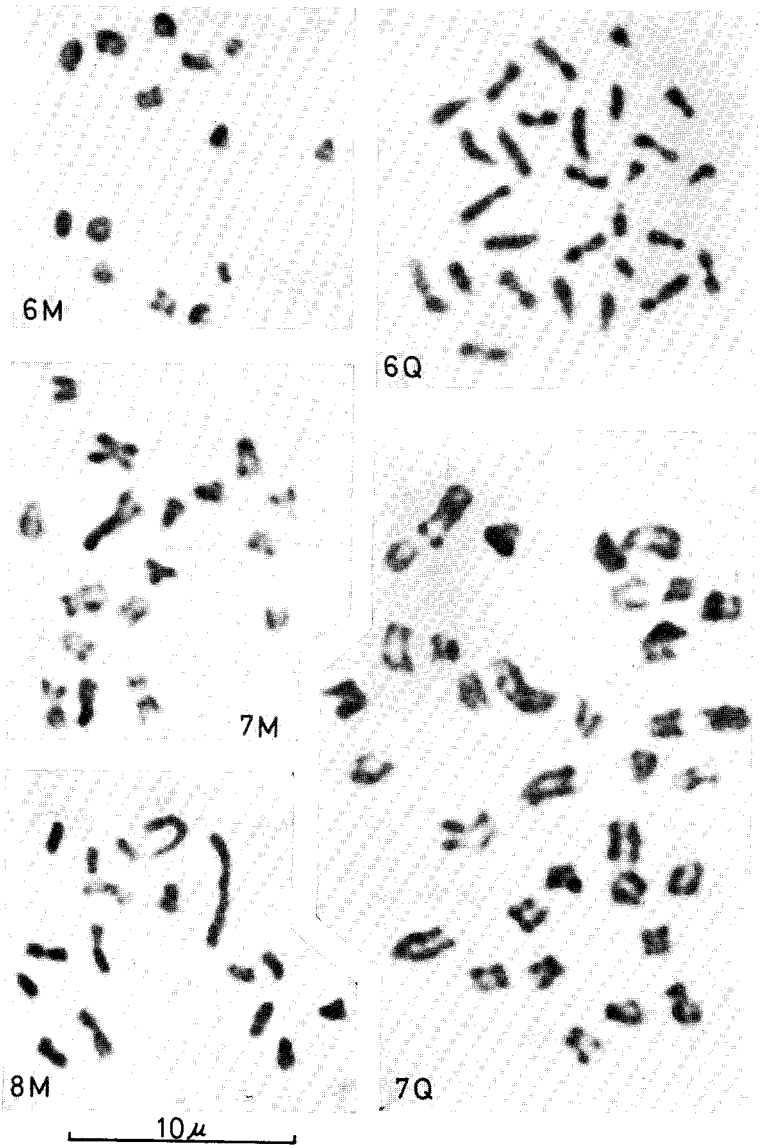
Plate 5

Fig. 17. *Formica sanguinea* 17M (♂, testis) n=26; 17Q (queen, ovary) 2n=52.
Fig. 18. *Formica japonica* 18M (♂, testis) n=27; 18Q (queen, ovary) 2n=54.

Plate 1

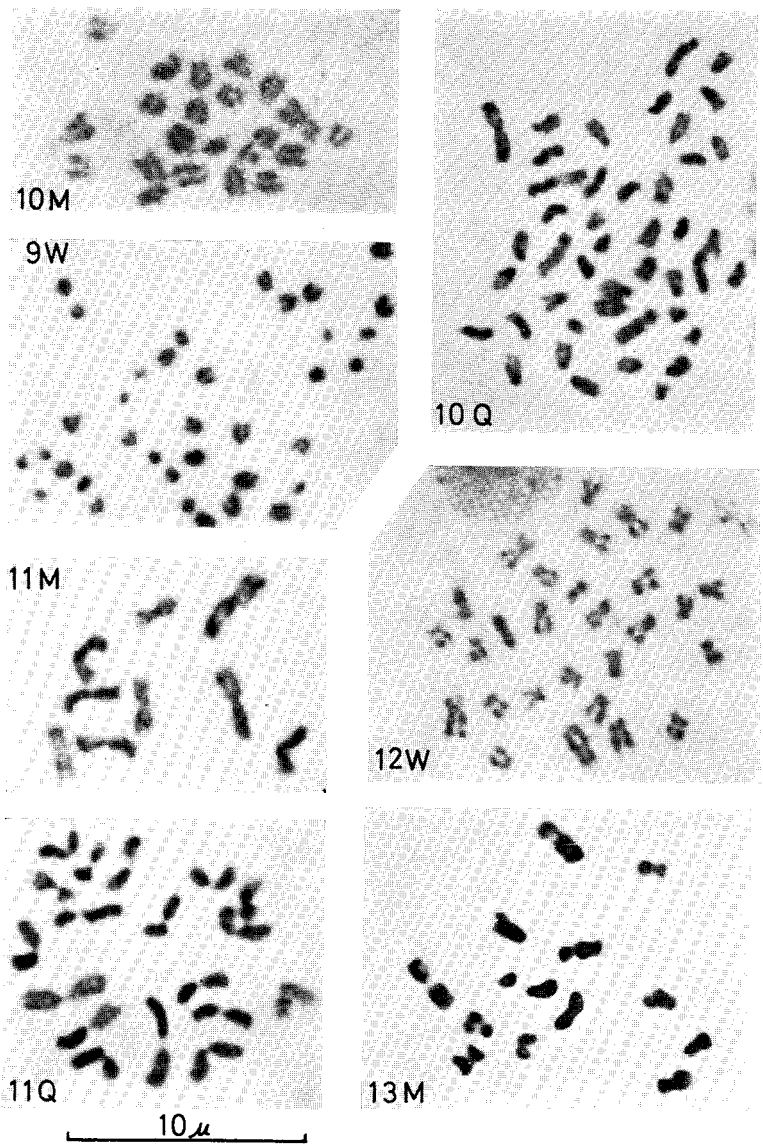


Chromosomes of ants



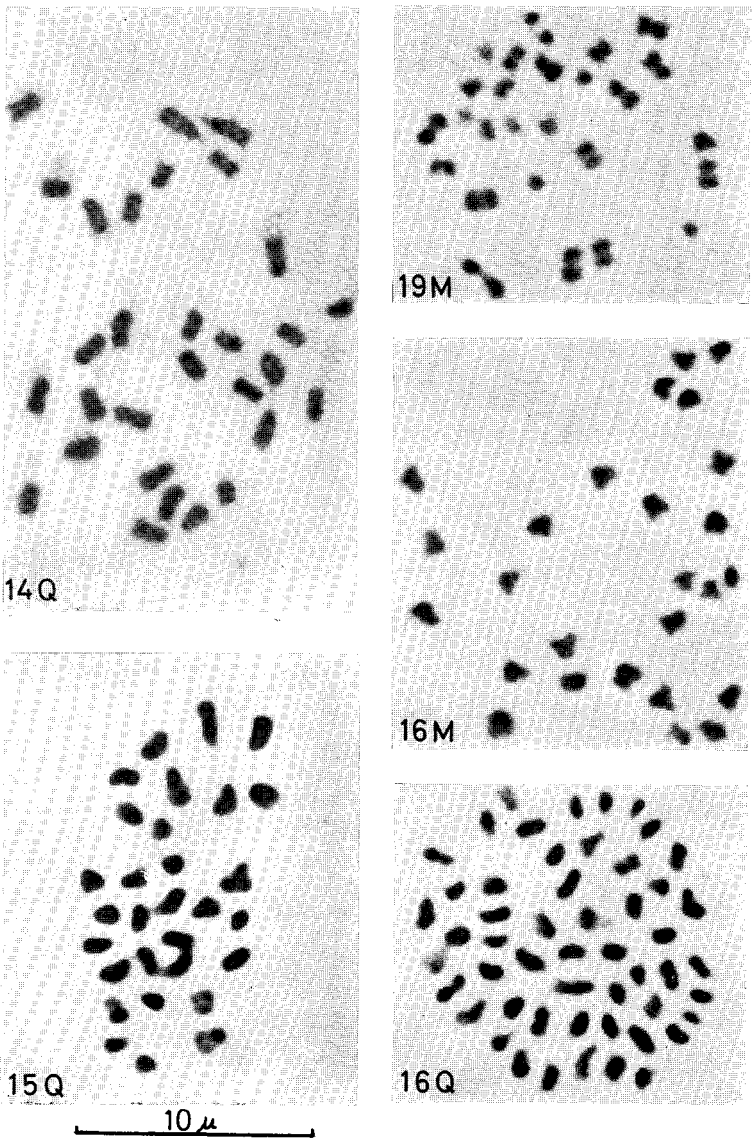
Chromosomes of ants

Plate 3



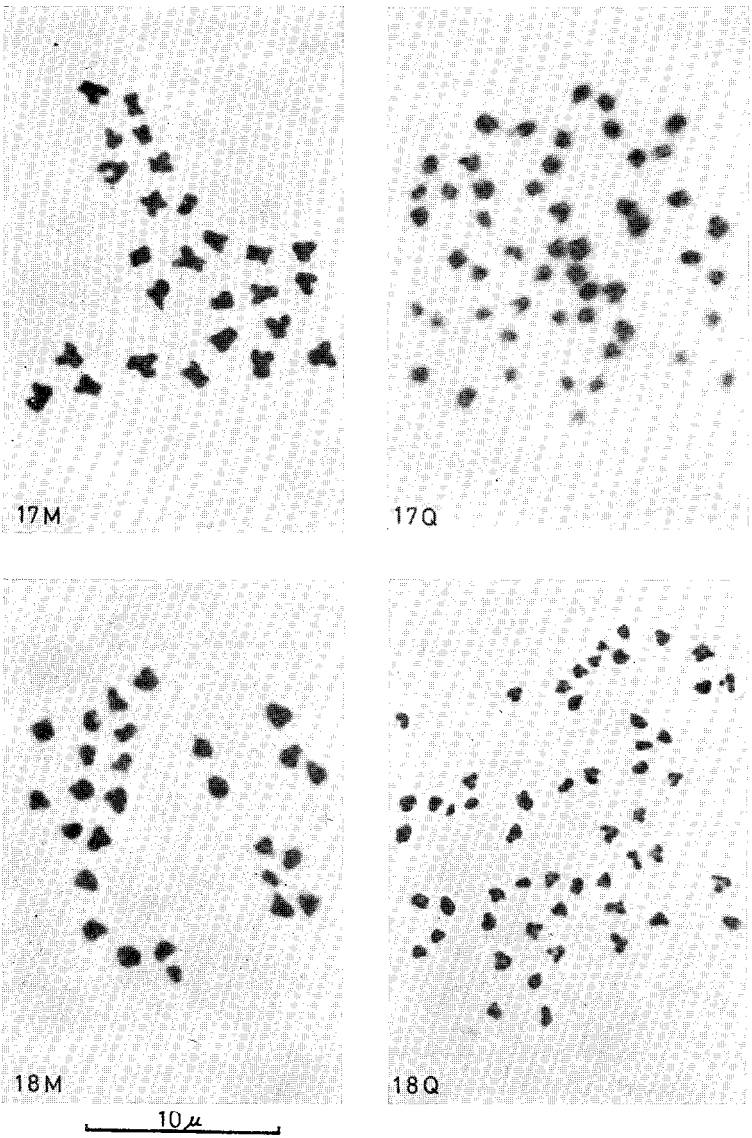
Chromosomes of ants

Plate 4



Chromosomes of ants

Plate 5



Chromosomes of ants