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Studies on Sterility in Hybrid Birds. IV. Cytological Researches on Hybrids in the Family Phasianidae

By

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With 3 Tables, 87 Textfigures and 15 Plates (79 Figures)

Contents

	PAGE
Introduction	309
Material and Methods	310
Review of cytological investigations on the hybrid in animals	312
PART I. Accounts regarding the hybrids between the Domestic fowl, <i>Gallus gallus</i> var. <i>domesticus</i> and the Common Pheasant, <i>Phasianus colchicus</i>	316
(1) Anatomical and histological observations on the reproductive organs in the hybrid birds	318
(a) The hybrid between <i>Gallus gallus</i> var. <i>domesticus</i> (Red-hackled Shamo) ♂ and <i>Phasianus colchicus karpowi</i> ♀	319
(b) The hybrid between <i>Phasianus colchicus versicolor</i> ♂ and <i>Gallus gallus</i> var. <i>domesticus</i> (Shamo) ♀	322
(c) The hybrid between <i>Phasianus colchicus versicolor</i> ♂ and <i>Gallus gallus</i> var. <i>domesticus</i> (Chabo) ♀	323
(2) Chromosome studies on the parental species and their hybrids	323
(a) Chromosomes of the Domestic fowl, <i>Gallus gallus</i> var. <i>domesticus</i>	324
(b) Chromosomes of the Common Pheasant, <i>Phasianus colchicus</i>	326
(c) Morphological comparison of the chromosomes between the Domestic fowl, <i>Gallus gallus</i> var. <i>domesticus</i> and the Common Pheasant, <i>Phasianus colchicus</i>	330
(d) Chromosomes of the hybrid between the Domestic fowl, <i>Gallus gallus</i> var. <i>domesticus</i> and the Common Pheasant, <i>Phasianus colchicus</i>	332

	PAGE
(e) Morphological analysis of the hybrid chromosomes	334
(3) Behaviour of germ-cells in the F ₁ hybrid	338
(a) Spermatogonial and oogonial divisions in the embryonal gonads	338
(b) Spermatogonial divisions in the adult testis ...	339
(c) The meiotic phenomena in the adult testis	340
(d) Degeneration of the oocytes in the embryonal ovary	341
(4) Discussion	341
PART II. Accounts regarding the hybrids between the Japanese Copper Pheasant, <i>Syrnaticus soemmerringii</i> and the Golden Pheasant, <i>Chrysolophus pictus</i>	344
(1) Anatomical and histological observations on the reproductive organs in the hybrid birds	345
(2) Chromosome studies on the parental species and their hybrids	347
(a) Chromosomes of the Hondo Copper Pheasant, <i>Syrnaticus soemmerringii scintillans</i>	347
(b) Chromosomes of the Golden Pheasant, <i>Chrysolophus pictus</i>	348
(c) Morphological comparison of the chromosomes between the Japanese Copper Pheasant, <i>Syrnaticus soemmerringii</i> and the Golden Pheasant, <i>Chrysolophus pictus</i>	349
(d) Chromosomes of the hybrid between the Japanese Copper Pheasant, <i>Syrnaticus soemmerringii</i> and the Golden Pheasant, <i>Chrysolophus pictus</i> ..	350
(e) Morphological analysis of the hybrid chromosomes	352
(3) Behaviour of germ-cells in the F ₁ hybrid	354
(a) Spermatogonial division in the adult testis	354
(b) The first meiotic division	354
(c) The second division	355
(4) Discussion	357
PART III. Accounts regarding the hybrids between the Golden Pheasant, <i>Chrysolophus pictus</i> and the Lady Amherst Pheasant, <i>Chrysolophus amherstiae</i>	362
(1) Anatomical and histological observations on the reproductive organs in the hybrid birds	363
(2) Chromosome studies on the parental species and their hybrids	364
(a) Chromosomes of the Lady Amherst Pheasant, <i>Chrysolophus amherstiae</i>	364
(b) Chromosomes of the hybrid between the Golden Pheasant, <i>Chrysolophus pictus</i> and the Lady Amherst Pheasant, <i>Chrysolophus amherstiae</i> ..	365

	PAGE
(c) Morphological analysis of the hybrid chromosomes	367
(3) Behaviour of germ-cells in the F ₁ hybrid	368
(4) Discussion	369
Conclusion	372
Summary	373
Literature cited	376

Introduction

In the case of animals the hybrids, either interspecific or intergeneric, are generally sterile without producing progenies. The cytological investigations of the hybrids are on the whole less extensive in animals than in plants where a number of valuable works have been appeared on this subject. The works on the species hybrids of the Lepidopterous insects made by Federley ('13, '14) and those of *Drosophila* by Sturtevant ('20, '21, '29), Kerkis ('33) and Dobzhansky & Tan ('36) are probably the most remarkable studies in this line. With respect to the higher vertebrates, no accurate cytological research of hybrid sterility has hitherto been done, excepting some classical and incomplete works such as by Wodsedalek ('16) on the mule and by Cutler ('18) on *Phasianus* × *Gallus*. Encouraging the present author to make some contribution on the cytology of hybrid sterility, Prof. Oguma of the Hokkaido Imperial University suggested him to undertake a new study in the avian hybrids which are rather easy in production between either species or genera and in most cases sterile. Since 1939 the work has been continuously carried on under his close guidance and with his kind cooperation, and three papers have already been published on this subject in the series of studies (cf. Yamashina, '40, '41a, '41b). In the present report some accounts will be given of the hybrids produced in the crosses between some gallinaceous birds.

The present study consists of three parts. Part I is concerned with the accounts of the intergeneric hybrids between the Domestic fowl, *Gallus gallus* var. *domesticus* and the Common Pheasant, *Phasianus colchicus*, which are completely sterile. Since Frisch (1775) a number of hybrids from this cross have been recorded (Leadbeater, Henslow, Fuller, Niemeyer, Renner, Suchetet, Ogilvie-Grant, Cronau, Guyer, Wheeler, Heinroth, Poll, Cutler, Taibell, Low, Sandnes & Landauer Danforth & Sandnes, Kuroda). Referring to

the literature there are found a few classical works published on cytology of this hybrid (Poll '10, '12, Cutler '18), but all of them seem very far from correctness in the light of the present knowledge, many important points remaining entirely obscure. Part II involves the results from the intergeneric cross between the Japanese Copper Pheasant, *Syrnaticus soemmerringii* and the Golden Pheasant, *Chrysolophus pictus*. In the systematic relation, these parental birds are rather close with each other as compared with the relation existing between *Gallus* and *Phasianus*. Their hybrids are found to be partially fertile in the male, normal spermatozoa being produced in an extremely small proportion, and the female are completely sterile with quite rudimentary genital organs. Part III deals with the interspecific hybrids produced between very closely related species, the Golden Pheasant, *Chrysolophus pictus* and the Lady Amherst Pheasant, *Chrysolophus amherstiae*. The hybrids from this cross are found to be completely fertile and produce fertile offsprings from generation to generation. The cytological phenomena observed in the hybrid gonads show no slight evidence different from those found in pure normal birds.

The evidences obtained in this study together with those presented in the foregoing studies (Yamashina '40, '41a, '41b) present a continuous series of grade in sterility. After referring to all cases studied some efforts have been made in this paper to explain the cause of hybrid sterility of this kind from the standpoint of cytology.

Before going further, it is the writer's pleasant duty to acknowledge here his greatest indebtedness to Prof. K. Oguma, the Dean of the Faculty of Science, Hokkaido Imperial University, by whose suggestion the present investigation was started and who has given the enthusiastic and expert guidance and laboratory facilities during the course of this work.

Material and Methods

The birds employed as the material are as follows:

1. The hybrids came from the cross between the Shamo (the Japanese Game) ♂ and the Korean Ring-necked Pheasant, *Phasianus colchicus karpowi* ♀. All the specimens including adult, young and embryonal individual were produced in the author's aviary in Tokyo. Details on the morphological and ecological accounts of these hybrid birds were given in the author's previous paper (Yamashina '42b).

2. A single hybrid specimen between the Japanese Green Pheasant, *Phasianus colchicus versicolor* ♂ and the Shamo ♀ employed for this study was bred by Mr. K. Kitada in Saitama Prefecture.

3. A single hybrid obtained between the Japanese Green Pheasant, *Phasianus colchicus versicolor* ♂ and the Chabo (the Japanese Bantam) ♀ employed for this study was specially bred by Mr. Kiyota in Ōsaka for the purpose of the present study.

4. The hybrids produced between the Hondo Copper Pheasant, *Syrnaticus soemmerringii scintillans* ♂ and the Golden Pheasant, *Chrysolophus pictus* ♀ were bred by Mr. S. Nomura in his aviary in Tokyo.

5. A single male hybrid from the cross between the Golden Pheasant, *Chrysolophus pictus* ♂ and the Lady Amherst Pheasant, *Chrysolophus amherstiae* ♀ employed for this study was F₁ hybrid bred in Marquis Hachisuka's aviary in Tokyo.

6. The material of *Phasianus colchicus karpowi* and *Phasianus colchicus versicolor* was obtained by the courtesy of Dr. S. Uchida from the aviary of the Nōrinsyō Tyōzū-Zikkensyō at Renkōzi.

7. The Hondo Copper Pheasant, *Syrnaticus soemmerringii scintillans* employed were wild birds captured in Tochigi Prefecture.

8. The Golden Pheasant, *Chrysolophus pictus* and the Lady Amherst Pheasant, *Chrysolophus amherstiae* employed were obtained from a bird-dealer in Tokyo.

9. The Domestic fowls of various races employed were mostly furnished through generosity of Mr. T. Mitsui, and some by Messrs. T. Kōno, T. Senba and some other gentlemen.

Here the author wishes to express his cordial thanks to these gentlemen who kindly placed these valuable specimens at the author's disposal.

For the histological study of the genital organs, especially in the female, the tissues preserved in 10% formalin or Bouin's fluid were employed as material. In this case the material treated through ordinal paraffin method were stained with Delafield's haematoxylin with counterstaining of eosin.

For the study of chromosomes in the spermatogonial and oogonial cells, the gonads taken from 11-13 days embryos by vivisection were mainly used for the material, in some cases the testes of the adult birds being employed. The embryonal gonads were exclusively fixed with Hermann's mixture and those of adult birds were preserved in Champy's solution modified by Dr. S. Makino, and sometimes in Hermann's solution. The preservation of the material was made with cooperation of Dr. Makino in all cases. Following the usual treatment of the paraffin method, the material was cut at varying thickness from 6 to 12 micra and stained

following to the iron-haematoxylin method after Heidenhain with a counterstaining of light green. The study of the spermatocyte chromosomes and of the meiotic process was made in the adult testes by the above treatment.

With the special purpose of tracing the process in spermioteleosis, some other fixing and staining methods were tried in order to give a sharp differentiation of the nucleic and cytoplasmic elements. For this purpose Mann's, Altmann's and Champy-Kull's procedures were adopted.

The figures of chromosomes indicated in this paper were originally drawn with the aid of a Zeiss Camera lucida using a 30 × comp. eyepiece and 1.5 mm. apochr. objective, at a magnification of 5000 times, unless otherwise noticed. The figures were reduced in printing, the reduced magnification being given in each figures. All the microphotographs annexed in this paper were kindly prepared Dr. Makino. Here the author must express his hearty thanks and acknowledgement to Dr. Sajiro Makino who never felt tired of helping the author throughout this investigation, and without whose cooperation this study could never have been accomplished. The author also wishes to express his obligation for kind assistance given by Messrs. S. Tarao and H. Niiyama in the course of this work.

Review of cytological investigations on the hybrid in animals

The cytological investigations on the hybrids are generally less extensive in animals than in plants, but there are a few investigations concerning the hybrid of insects. Federley ('13, '14, '31) firstly described the behaviour of the germ-cells in the hybrid between certain species of moths belonging to the genus *Pygaera*. According to him, the chromosomes of the parental species frequently fail to pair at meiosis in the sterile and semi-sterile hybrids. The species *Pygaera anachoreta*, *P. curtula*, and *P. pigra* have 30, 29, and 23 chromosomes in haploid respectively; the hybrids contain in their tissues the total sum of the haploid number of parental species. Most chromosomes remain univalent in the hybrid testis. In *Pygaera* hybrids, the univalents split at both meiotic divisions, and the spermatids tend to possess the somatic number of chromosomes. Various abnormalities (fused spindles, failure of cell divi-

sion, etc.) are observed in the spermatocytes and the spermatids usually undergo degeneration. The hybrids are semi-sterile.

Goldschmidt ('32, '34) made genetic analysis of the hybrids between the local races of *Lymantria dispar*, and in this case the sterility is considered to be due to the action of complementary genetic factors. Pariser ('27) reported the hybrid between certain species of the moth belonging to the genus *Saturnia*. The F_1 progenies are mostly intersex. *Saturnia pavonia* and *Saturnia pyri* have 29 and 30 chromosomes in haploid respectively. The F_1 hybrid has 59 chromosomes, most of which fail to form bivalents at meiosis. Dobzhansky ('37) considered that this hybrid may be a type of genetic sterility in contrast with the triploid intersex found in the *Drosophila* hybrid.

The important studies with *Drosophila* crosses have been made by Sturtevant ('20, '21, '29), Kerkis ('33), Dobzhansky & Tan ('36) and some others. According to Kerkis ('33, '36) *Drosophila melanogaster* and *Drosophila simulans* possess metaphase chromosomes which appear quite identical each other under the microscope, whereas the hybrids between them are completely sterile. The gonads are rudimentary, and spermatogenesis and oogenesis do not advance beyond spermatogonia and oogonia. According to the comparative genetical work on *Drosophila melanogaster* and *Drosophila simulans* made by Sturtevant, the arrangement of genes is different between these species. The chromosomes of females of *Drosophila pseudoobscura* and *Drosophila miranda* are also identical each other when seen in the metaphase, but the hybrids between these species are sterile. According to Dobzhansky & Tan ('36) gene arrangement of these species is profoundly different, and most nuclei in this hybrids show only a few chromosomes paired. The investigations on the hybrid between race A and race B of *Drosophila pseudoobscura* also give a great contribution to this subject. According to Lancefield ('29) race A and race B of *Drosophila pseudoobscura* possess quite the same chromosome complex, but the cross race B ♀ × race A ♂ gives in F_1 sterile male with small testes; the reciprocal cross race A ♀ × race B ♂ produces sterile male that has testes of normal size. According to Dobzhansky ('34) the sterility of this hybrid is due to a profound modification of the process of spermatogenesis. The meiotic chromosome pairing is variable; no univalents, some univalents, or only univalents may be present at

the first meiotic division. Irrespective of the number of the bivalents and univalents formed, only a single meiotic division takes place, which is characterized by an anomalous behaviour of the spindle. The spermatids degenerate without being transformed into spermatozoa. Dobzhansky ('36) stated that the fertility or sterility of this hybrid does not depend upon the ultimate source of their cytoplasm, but upon their chromosomal constitution. The hybrid males having all chromosomes of the same race, or having one third or one fourth chromosome of the opposite race from the rest of the chromosomes, are fertile. But if both the third and fourth chromosomes disagree in racial origin with the rest of the complement, the male is sterile. According to Dobzhansky ('36) sterility of these hybrids must be a type of genic sterility.

Excepting the insect, the mammals have often been offered as the material for the investigation of the hybrid sterility. As the classical example of this is found in the work of Wodsdalek ('16) on the mule which is the sterile hybrid between the horse, *Equus caballus* and the ass, *Equus asinus*. He showed, as the cause of sterility, the difference of the chromosome complex in the parental species. According to Painter ('24) and Meladze ('37), however, the karyotypes of the horse and the ass are quite similar. About the cause of sterility in the mule, therefore, a reinvestigation study is required. A similar condition seems to occur in the hybrid between the Domestic cow, *Bos taurus* and the Yak, *Poephagus grunniens*, which is proved to be completely sterile. According to Krallinger ('31) the chromosome number of the domestic cattle is certainly 60 and recently Zuitin ('38) reported the same chromosome complex, quite similar in number, to exist in the yak. The behaviour of the germ-cells in these hybrids, however, has not been studied. The hybrid between arkhar (*Ovis pollii karelini*) and Kurdiuchny ram (*Ovis steato pyga*) has been known to be fertile and the chromosome number in the hybrid and the original forms is identical, being 60 in diploid and 30 in haploid. Similar evidence was recently revealed to exist in the species hybrid of mice, *Mus musculus* × *Mus molossinus* (Makino '41). The results reported by Painter ('27) on the interracial hybrid between Gates' "non-disjunction" (v-o) mice and Japanese waltzing mice were reexamined by Makino ('41) and found to be entirely invalid.

Here an historical sketch will be made on the studies on avian

hybrids. In fact, birds produce the hybrids most easily. According to Hopkinson ('26, '30-41) more than 600 combinations of the hybrid were actually produced by the aviculturists, and many inter-generic, inter-subfamily, and even so-called interfamilial hybrids are found among them. Such hybrids between quite distantly related parents might be quite difficult to produce in other animals. Very early Henslow (1834) and Suchetet (1897) reported that the spermatozoa were never produced in the hybrid between the Domestic fowl and the Pheasant, though the seminal tubules of that hybrid were normal. Guyer published a paper in 1900, in which he suggested that the deformed spermatozoa of the sterile hybrid pigeon are due to the abnormality of the spindle, which causes the difference of distribution of chromatin. Poll ('10) described, after having worked on the testis of the hybrid between *Phasianus colchicus* ♂ × *Gallus gallus* var. *domesticus* ♀, that the germ-cells did not develop beyond the stage of the spermatogonia. In the further study published in 1912, he found that some of the germ-cells in the hybrid testis grow up to the synapsis stage. Cutler ('18) was the pioneer investigator who described the cytological evidences on the hybrid of this kind, but his observations approached to no exactness with unsatisfactory results, due to the technical difficulties. He arrived at the conclusion that the abnormality occurred in the synizesis stage was resulted in the lack of affinity of the parental chromosomes during meiosis. Comparatively recent studies are those carried by Sokolowskaja ('35) and Crew & Koller ('36) on the hybrid between *Cairina moschata* and *Anas platyrhynchos*. In these studies, especially in the latter, a karyotype of the parents and the hybrid was proposed. According to Sokolowskaja the karyotype of this hybrid is quite the same as that of the parental forms, only the largest and second largest elements being of V-shape, and sex-chromosomes are represented by the third largest rod-shaped chromosomes. According to Crew & Koller, however, sex-chromosomes are represented by the largest V-shaped chromosomes and maximum number of the chromosomes counted by them was 70. But the karyotypes suggested by these workers were found out to be fully erroneous by the author's previous study ('41b), in which the chromosome numbers of the parents and their hybrids are decided to be 80 (♂, 2n) and 79 (♀, 2n) and the sex-chromosomes are decided to be fifth largest rod-shaped chromosomes. As for the cause of the sterility Crew & Koller

ascertained that the sterility of the hybrid is due to complementary genetic factors which do not affect chromosome pairing but which disturb and alter its relationship with spindle development; but this was found out to be erroneous. According to the author's previous study, the cause of the sterility lies in the failure of the pairing of the homologous chromosomes, leading to irregular meiotic division (Yamashina '41b).

In the present paper the cytological accounts are given on the following three hybrids; *Gallus gallus* × *Phasianus colchicus*, *Syrnaticus soemmerringii* × *Chrysolophus pictus*, and *Chrysolophus pictus* × *Chrysolophus amherstiae*. The results obtained in this study, in connection with those secured in the previous investigations (Yamashina '41a, '41b), seem to offer some new finding for interpretation of the cause of hybrid sterility in animals.

Part I. Accounts regarding the hybrids between the Domestic fowl, *Gallus gallus* var. *domesticus* and the Common Pheasant, *Phasianus colchicus*

On account of the fact that the cross between the Domestic fowl and the Common Pheasant is rather easy in captivity, the hybridization between these two genera frequently occurs in those days, the record thereof having been occasionally known. The first author who recorded the hybrid offsprings of this cross in the recent ornithological literature seems to be Frisch (1775), and in that time, according to him, these hybrids seem to have been produced not rarely in Europe, especially in Germany, as a food bird. Later in the 19th century the breeding of these hybrid birds is apparently confined to some bird-lovers or investigators for a special purpose.

In the crossing experiments between the Domestic fowl and the Common Pheasant attempted by the present author during the years of 1939 to 1940, using the different combinations of the parent birds, 164 hybrid eggs in total were obtained. After incubation, it was proved that 46 eggs among them were shown to be fertilized, from which 9 unhatched embryos, 12 chicks and 9 adult birds came under our observation. The combinations and their offsprings are shown in the following table.

Table 1

Combinations and their offsprings employed for the observation

Parents	Offspring		
	Adults	Chicks	Embryos
<i>G. g. var. domesticus</i> (Shamo) ♂ × <i>Ph. c. karpowi</i> ♀	8♂♂, 1♀	5♂♂, 7♀♀	1♂, 5♀♀
<i>G. g. var. domesticus</i> (Shamo Bantam) ♂ × <i>Ph. c. karpowi</i> ♀ . .	—	—	3
<i>Ph. c. versicolor</i> ♂ × <i>G. g. var.</i> <i>domesticus</i> (Shamo) ♀	1♂	—	—
<i>Ph. c. versicolor</i> ♂ × <i>G. g. var.</i> <i>domesticus</i> (Chabo) ♀	1♂	—	—

In the 46 fertilized eggs obtained, the sex was determined of all unhatched hybrid embryos,* and of all birds which died after hatching or which were killed at later stages for observations, as shown in the following table.

Table 2

Sex ratio obtained from 46 fertilized eggs

Stages	Sex		
	♂	♀	Not determined
Embryos	1	8	12
Chicks	5	7	4
Adults	8	1	—
Total	14	16	16

Reviewing the above table it is evident that among the hybrid offsprings of these crosses, the sex ratio is nearly 1 to 1. The unusual excess of males among the similar crosses as reported by other authors (Poll '12, Cutler '18, Taibell '32, etc.) seems to be derived from observations on the adult. It seems probable from the author's experiments, that the mortality of female hybrids is very high during the incubation and also in the chicks just after hatching.

The detailed accounts on the records of breeding, the mor-

* In the majority of this case, the sex was determined by the actual observations of the sex-chromosome in germ-cells of the embryonal gonads.

phology and plumage of the hybrid birds, and some other oecological observations were given in the author's previous paper (cf. Yamashina '42).

The fact that the generic cross between the fowl (*Gallus*) and the pheasant (*Phasianus*) produces always completely sterile offsprings with no sexual behaviour has been known, and Suchetet (1897) seems to be the first who described this fact on the basis of microscopical observations, in which no spermatozoa were produced in the seminal tubules of the testes of the hybrid birds, and in the female the ovary and oviduct are very rudimentary in structure. As mentioned in the foregoing chapter Poll ('10, '12), working on the testis of the hybrid between *Phasianus colchicus* ♂ × *Gallus gallus* var. *domesticus* ♀, described that some of the germ-cells in the hybrid testis grow up to the synapsis stage. Cutler ('18) was the pioneer investigator who described the cytological evidences of the hybrid of this kind, but his observations due to the technical insufficiency, reached the unsatisfactory results lacking the accuracy. He entirely failed to observe the number and other morphological characteristics of the hybrid chromosomes, except that the spermatogonia multiply by division and the auxocytes do not advance beyond the synizesis stage because of abnormality. He arrived at the conclusion that the abnormality occurred in the synizesis stage was resulted in the lack of affinity of the parental chromosomes during meiosis. Needless to say that the conclusion drawn by him is not based on the accurate cytological observations.

(1) *Anatomical and histological observations on the reproductive organs in the hybrid birds*

The anatomical and histological investigations on the gonads of the F₁ hybrids derived from the cross between *Gallus gallus* var. *domesticus* and *Phasianus colchicus* were early made by Suchetet ('97) Poll ('10, '12), Cutler ('18), and some others. They reported that the testes of the F₁ hybrid are normal in shape but very small, and that the ovary is rudimentary in structure, with the egg cells undeveloped. The present studies made upon the material derived from the cross of various sorts revealed similar but more affirmative evidence.

- (a) The hybrid between *Gallus gallus* var. *domesticus*
(Red-hackled Shamo) ♂ and *Phasianus*
colchicus karpowi ♀

The observations were made on the material from 8 males and 8 females hybrids, derived from this cross. They consist of 8 embryos, 1 ♀ newly hatched, 1 ♀ of 30 days old, 2 ♂♂ of 6 months old, 1 ♂ of 10 months old, 1 ♀ of 12 months old, 2 ♂♂ in 22 months old, and 2 ♂♂ in 24 months old. The last 2 males were dissected after having been injected with 0.5 cc. Testosteron and 0.5 cc. Puberogen, 6 times in each other day.

Male embryos. The dissection of 11 days embryos shows that their testes are at the regular position with normal development and the section of the testis indicates that the seminal tubules develop as regularly as found in the bird of pure line (Pl. XXVI, figs. 15, 16), each seminal tubule consisting of the spermatogonial cells. They are all in the process of active division, which proceeds quite normally. A number of dividing figures were observed, of which the detailed morphological studies of chromosome were made as given in the later section.

6 months old males (Nos. 45, 46, fixed in December, 1939). The hybrid herein dealt with are young birds in the first winter plumage, but they are hardly distinguishable from the adult bird either in their size or in their colour of plumage. Though quite rudimentary, a pair of testes were in the normal position, measuring 9×2.5 mm. (right side) and 12×4 mm. (left side) in specimen No. 45, and 9×2.5 mm. (right side) and 11×3 mm. (left side) in No. 46 (Pl. XXVI, fig. 17). The section shows that the development of the seminal tubules was very poor, the tubule being lined by one or two layers of spermatogonial cells, remaining a narrow lumen in the central space (Pl. XXVI, fig. 18). The structure nearly resembles the testis of 30 days old chick, its diameter also being similar. The division of the spermatogonia is quite inactive, and the cells in division numbering two or three in a dozen of seminal tubules. Two or three auxocytes in the early growing period were also found in several dozen tubules. From the histological viewpoint the vas deferens seems to be normal, but no sperms were found within it (Pl. XXVI, fig. 19).

10 months old male (No. 75, fixed in April, 1940). In this bird, dissected in the breeding season, the testis was a little larger than

that of the 6 months old male, the measurements of the testes showing 10.5×3 mm. (right side), and 15.5×2.5 mm. (left side). As compared with that of the normal bird, the size of the testes mentioned above is relatively small. After sectioned, the structure of the seminal tubules was found to be not different from that of the 6 months male already noted, the diameter of each tubule also being almost similar to that of the latter. One or two layers of the spermatogonial cells were found lining the tubules, the dividing figure being quite scarce. The differentiation of germ-cells is, however, rather advanced, and several auxocytes proceeded to the stage of bouquet were found after examination of several seminal tubules. In a few cases there was found that the seminal tubules contain aggregations of auxocytes in bouquet stage (Pl. XXVII, fig. 20). However, the cells advanced to pachytene stage were very few in number in our examination.

22 months old male (No. 116, fixed in April, 1941). This bird, a full grown adult, was killed in the breeding season, and the testes were measured 9×4 mm. (right side) and 10×3 mm. (left side), being smaller than those of the 10 months old. The seminal tubules show no advanced development as compared with those found in the 10 months male and the germ-cells contained are also quite scanty (Pl. XXVII, figs. 21, 22). Noteworthy is the fact that the division figure of spermatogonia is less frequent, and the majority of cells advances to the stage of pachytene. Sometimes there appeared the cells which are in the process of degeneration in the tubules. By this evidence it may be understood that the testis of this bird is smaller than that of 10 months old bird. And, there is no doubt that the germ-cells do not differentiate beyond the stage of pachytene in the hybrid testis. With the degeneration of germ-cells, the testis seems to attain no more growth beyond this stage of development.

22 months old male (No. 155, fixed in March, 1942). Of the testes, measuring 13×3.5 mm mm. in the right side and 13×4 mm. in the left, sections do not show in the structural condition any significant difference from that observed in No. 116 mentioned above. The seminal tubules contain spermatogonial cells of resting condition lining inside in one or two layers. In some tubules there are observable aggregations of auxocyte in bouquet and pachytene stage, and some contain pycnotic cells which are in the course of degene-

ration. All the conditions consequently show that there occurs quite similar appearance in the testis of this individual. The vas deferens was found to be structurally normal in both side, so far observed in sections, but they contained no single piece of spermatozoa, being entirely empty (Pl. XXVII, fig. 23).

24 months old males (Nos. 119, 120, fixed in June, 1941). These two males, from the same clutch, were killed after hormone injection of Testosterone and Puberogen (for details, see p. 319). In both of the birds the testes were very small in size, and the measurement shows 7×2 mm. in each. Section indicates again the seminal tubules to be sterile development, just as the conditions found in Nos. 116 and 155, or sometimes they were in more advanced state of degeneration. On the other hand the most of germ-cells contained are found in resting condition or in the process of pycnotic degeneration. The interstitial cells, on the contrary, were found well developed between every seminal tubules (Pl. XXVII, fig. 24). The supposition may be made that the degeneration of germ-cells was accelerated by injection of sex hormone (cf. Yamashina '42).

Female embryos. The ovary of 11 days old embryo was normal in general aspect as shown in Pl. XXVIII, fig. 25 and section shows that many oogonial cells in the process of division were found in the germinal epithelium. The behaviour of chromosomes in division is quite normal, and a number of well fixed metaphase figures were found in which the detailed studies of morphology of chromosomes were undertaken as given later.

Female chick newly hatched. The external feature of the ovary, and the histological structure were on the whole normal in the chick. The condition of the ovary nearly resembles in size and shape to that of the chick of parental form in the same age. It is noticeable that the ovary of this chick is a little larger in comparison with that of the adult females, and in sections it was seen that the germinal epithelium contains many germ-cells, *i.e.*, oocytes as occurred in the ovary of parental form in the same age. The difference is noticed in the fact that the oocytes contained are advanced to leptotene stage in parental birds having large nuclei, while in the hybrid the nuclei are small, the majority of them taking the course of pycnotic degeneration (Pl. XXVIII, figs. 26, 27). Thus it is possible to see that the female germ-cells are in course of degeneration in the hybrid, during the later part of the embryonal stage.

30 days old female (No. 28230). The ovary of this hybrid bird contains no follicles of normal structure, though in the normal female chick of the same age the formation of follicles has already occurred. The atrophic degeneration of germ-cells seems to be more proceeded in this individual, and from this evidence it is likely that the development of ovary in the hybrid bird ceases early in this stage. This fact is also suggested from the observation on the ovary of the twelve months old individual noted in the next section.

12 months old female (No. 127, fixed in July, 1941). This bird was a deformed individual, its plumage being imperfectly developed, and the sex was not decided from the examination of the external characters (for detailed descriptions, see the author's previous paper published in Jap. Journ. Genet., 18 '42), but the bird was confirmed to be a female by the existence of ovary. Sections of the ovary revealed that it contains almost no follicle of normal form, and the histological condition assumes a resemblance in every respect to that of the 30 days old individual mentioned above (Pl. XXVIII, figs. 28, 29; Pl. XXIX, fig. 30).

Considered from the evidence mentioned above, it may be possible to summarize that the degeneration of germ-cells in the ovary has begun before hatching and the process of degeneration proceeds for a month after the hatching. Thus the ovary remains in the same stage for a little while, then afterwards there occurs the disintegration of the ovary itself.

The oviduct of this bird, though ordinal in position, was quite rudimentary in structure, developed only in the embryonal condition. Histologically, the opening of the fallopian tube was recognized (Pl. XXIX, fig. 32), but the epithelial structure of the oviduct remains in the embryonal condition in every respect (Fig. 31). Thus, with the disintegration of the ovary, this bird showed male-like appearance of plumage probably due to the lack of the ovarian hormone (cf. Yamashina '42).

- (b) The hybrid between *Phasianus colchicus versicolor* ♂
and *Gallus gallus* var. *domesticus* (Shamo) ♀

In this cross a single adult male (No. 71) was obtained, which was killed in April, 1940, in the age of 22 months old. By the dissection a pair of testes were found in the ordinary position in both

sides, measuring 9.5×4 mm. in the right side and 11×5 mm. in the left. Externally they are not different from those of the hybrid of Shamo ♂ \times *Phasianus colchicus karpowi* ♀ already noted. Sections showed that the dimension of seminal tubules was a little larger than that seen in the individual of the same age obtained from the reciprocal cross, and nearly similar to that of the 10 months old. The development of germ-cells in the testis further advanced than in the corresponding case of the reciprocal cross, and the first spermatocytes in the early stages of growing period were found in about a half of the seminal tubules observed. But these two hybrids from different crosses agree with each other in having none of germ-cells which advanced beyond pachytene stage (Pl. XXIX, figs. 33, 34).

(c) The hybrid between *Phasianus colchicus versicolor* ♂
and *Gallus gallus* var. *domesticus* (Chabo) ♀

Only one male specimen derived from this cross (No. 128) came under our observation, which hatched in May, 1940, and was killed in July, 1941, in the age of 14 months old. Differing from the other cross already described in which the development of testes attains thinner than the 24 months old hybrid from *G. g.* var. *domesticus* (Shamo) ♂ \times *Ph. c. karpowi* ♀. The spermatogonial cells are found along the wall of tubules forming a single layer. The cells in the division as well as the spermatocytes in the growing period were never observed in any part of the testis in this hybrid, while the interstitial cells, increased in number, were found here and there (Pl. XXIX, fig. 35).

(2) *Chromosome studies on the parental species
and their hybrids*

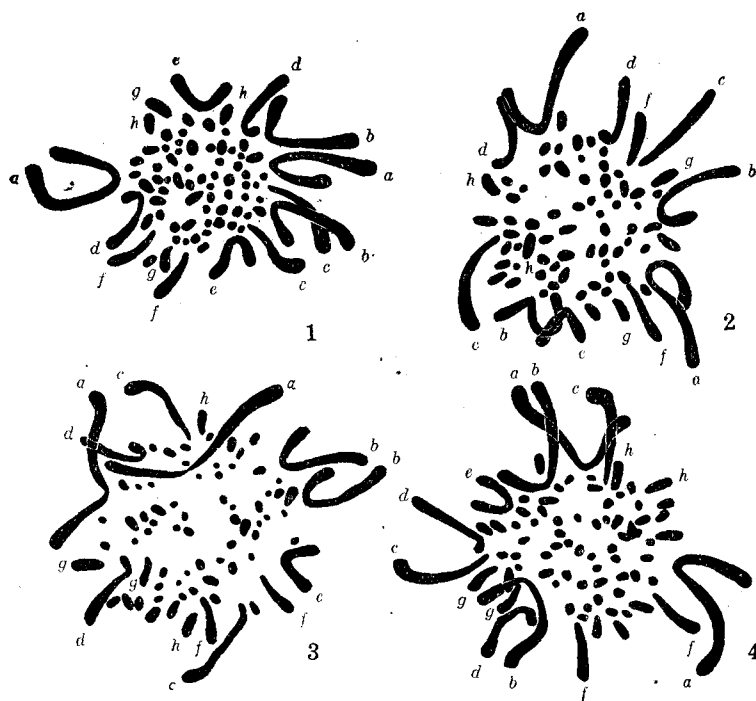
Reviewing the literature, one can see a number of papers which are concerned with the chromosomes of the fowl and the pheasant, but the exact knowledge of their chromosomes is achieved only from a few investigations recently attempted (Sokolov, Tiniakow & Trofimov '36, Oguma '38, Suzuki '39). In this study, the observations of the chromosomes in the parents were firstly made, followed by the study of hybrids.

(a) Chromosomes of the Domestic fowl, *Gallus gallus*
var. *domesticus*

Chromosomes of Domestic fowl was firstly studied by Loyez ('06) nearly half century ago followed by Sonnenbrodt ('08) and Guyer ('09), and since that time many cytologists have attempted the investigations on the same subject (cf. Oguma & Makino '37). Probably due to technical difficulties, however, all these classical workers failed to observe correctly the features of chromosomes either in the number or other morphological respects. Hance ('26) was probably the first investigator, who discovered that the chromosome complement of fowl consists of a certain number of V-shaped and rod-shaped chromosomes, with an uncertain number of minute granule-like micro-chromosomes. He proposed that the sex-chromosomes are represented by the largest V-shaped elements, numbering two in male and single in female. His statement was followed by Akkeringa ('27), Goldsmith ('28), White ('32) and Popoff ('33) by assuming the largest V-element as the sex-chromosome. Later, Sokolov, Tiniakow & Trofimov ('36) and Unger ('36) made a detailed analysis of the large-sized chromosomes and succeeded in the demonstration of the real sex-chromosome in the fowl. But these authors failed to determine the number of chromosomes. The confirmed number of chromosomes of the fowl was reported for the first time by Oguma ('38) and Suzuki ('39) to be $2n = 78$ in male and $2n = 77$ in female. The results of the present author's observations made upon various races of fowl are described in the following.

Spermatogonial chromosomes. A number of good metaphase figures of the spermatogonial division available for study were found in the embryonal testes taken from various races of the Domestic fowl. Pl. XXV, fig. 9 is a metaphase figure obtained in the Shamo, a race of the Domestic fowl on which the hybridization experiment were attempted in this study. The chromosome garniture as shown in the figure assumes a typical feature of the avian type, dividing into two distinct size-groups of larger (macro-) and smaller (micro-) chromosomes. The macro-chromosomes occupy the peripheral zone of the equatorial plate, and the micro-chromosomes scatter in the central region surrounded by the former, forming a beautiful rosette. By the careful examination the total number of chromosomes was determined to be 78 (σ , $2n$), in accordance with the counts recorded

by Oguma ('38) and Suzuki ('39). The macro-chromosomes are 16 in number (*a*'s-*h*'s in Textfig. 1), of which the four are extremely large and assume conspicuous V-shape forming two homologous pairs (*a*'s and *b*'s). The two chromosomes following them in size are telomitic in attachment, tapering at their inner terminals (*c*'s), and the other two following in size are of J-shape having subterminal attachment (*d*'s). The fifth largest chromosomes consist of two V-shaped elements (*e*'s), and form a homologous pair. The smaller six chromosomes (*f*'s-*h*'s) of macro-chromosomes are again telomitic rod-shaped like *c*'s, but they are much shorter. The micro-chromosomes all seem to be telomitic in structure and vary in shape from short rod to minute spheroid in a graded series.



Textfigs. 1-4. Chromosomes of *Gallus gallus* var. *domesticus* (♂ and ♀). ×4000. 1. Spermatogonial metaphase of the Shamo. 2. Oogonial metaphase of the Shamo. 3. Oogonial metaphase of the Shamo Bantam. 4. Oogonial metaphase of the Chabo.

Oogonial chromosomes. The female diploid chromosomes were exclusively studied in metaphase figures of oogonial division observed

in the embryonal ovaries of various races of the Domestic fowl. Pl. XXV, fig. 10 is a metaphase figure of oogonial chromosomes derived from the Shamo. The general aspect of the complex and the morphology of the individual chromosomes found in this figure shows a close resemblance to that already observed in the spermatogonium. But a close observation reveals that the macro-chromosomes number only 15 in the oogonium instead of 16 counted in male cells (Textfigs. 2-4). This results the total number of the female (oogonial) complex being 77, one fewer than that of the spermatogonial complement. The cause of this numerical difference lies in the fact that the fifth largest chromosome labelled *e* is destitute of its synaptic mate in the female cell as obviously recognizable in the serial alignments of chromosomes (Textfigs. 18-23). Thus the sexual difference of chromosomes is attributed to the fact that the fifth largest element *e* is always unpaired in the female cell, while in the male cell it is in a paired condition having a homologous mate. There is no doubt that the chromosome *e* under consideration is nothing other than the sex-chromosome. In this respect, the results reached in the present observation accord with those recorded by Sokolov, Tiniakow & Trofimov ('36), Unger ('36), Oguma ('38) and Suzuki ('39).

In the present report the chromosomes of three races, *Shamo*, *Shamo Bantam*, and *Chabo* were only described, all of them used for the crossing experiment. The investigation has been extended, however, with the kind cooperation of Prof. Oguma and Dr. S. Makino upon the following seven races, the *Ukokkei* (*Chinese Silky*), the *Uzura-chabo* (*Tailles Chabo*), the *Oshamo*, and the *Rode Island Red*, as well as the *White Leghorn*, the *Opington*, and the *Nagoya*. The observation shows that, so far as the general morphological characteristics are concerned, the chromosomes of all these races of the Domestic fowl are quite identical in all characters with one another, and that there is no visible difference in the chromosomes among the races observed, not only in number but also in other external feature. The detailed accounts on this respect will be published elsewhere with illustrations.

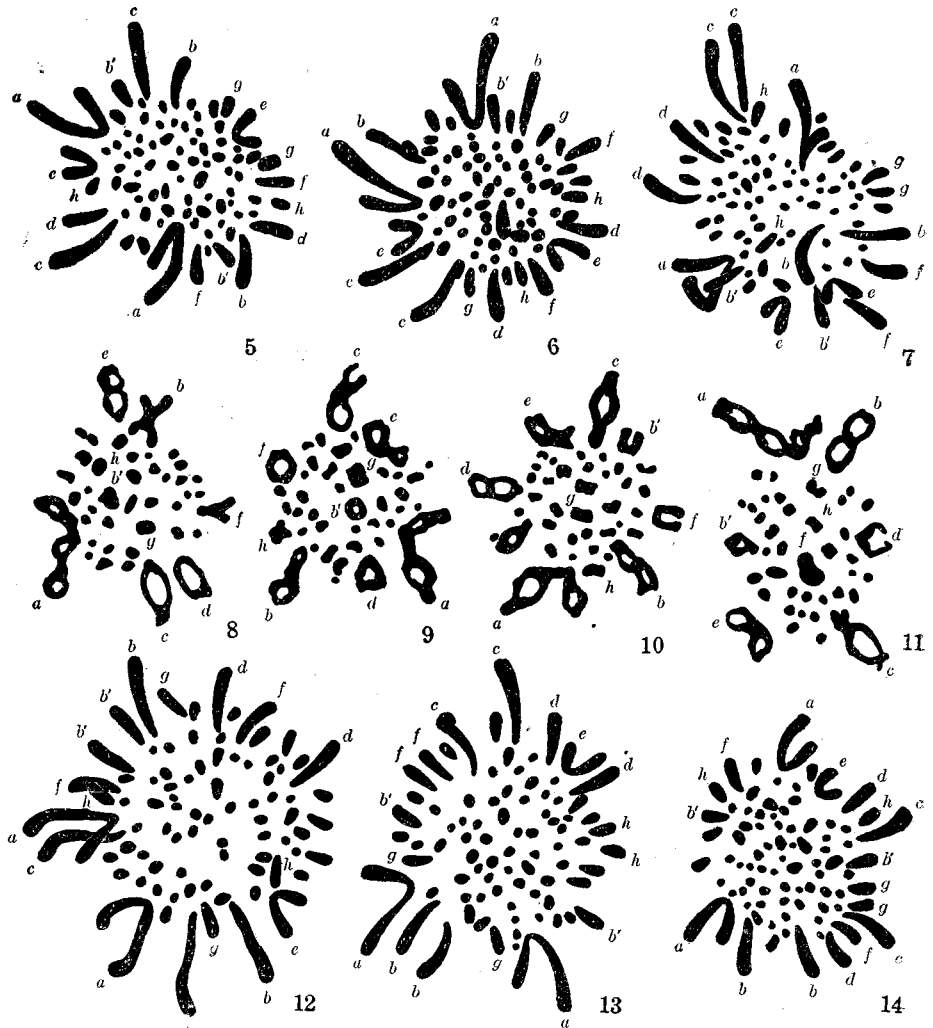
(b) Chromosomes of the Common Pheasant,
Phasianus colchicus

The chromosomes of the Common Pheasant were studied for

the first time by Cutler ('18), but due to technical difficulty, his study failed to show an accurate result. Recently Trofimov & Tiniakow ('33), Sokolov, Tiniakow & Trofimov ('36) studied the chromosomes of the Caucasian Pheasant, *Phasianus colchicus colchicus*, reporting that the chromosome number was found to be 40-63 in diploid and that the sex-chromosome is represented by the fourth largest element. Unger ('36), working on *Phasianus torquatus*, reached to a similar conclusion concerning the sex-chromosome, showing the chromosome number to be 52-61 in diploid. Quite recently Suzuki ('39) published a brief report on the observations of the chromosomes of the Korean Ring-necked Pheasant, *Phasianus colchicus karpowi*, in which the diploid number of chromosomes was informed to be 78 in the male and 77 in the female, and the sexual difference of chromosomes was established by the absence of a homologous mate in the fifth largest V-shaped pair in the female side. In the present study the number of chromosomes and other morphological characteristics were fully investigated, the result of which will be given in the following descriptions.

Spermatogonial chromosomes. The spermatogonial chromosomes were studied in the two subspecies, Korean Ring-necked Pheasant, *Phasianus colchicus karpowi* and Japanese Green Pheasant, *Phasianus colchicus versicolor*, both of which were used in the present hybridization experiment. A number of metaphase figures obtained in the embryonal testes from these two subspecies were investigated for determination of the chromosome number and the analysis of the morphological characters. Pl. XXV, figs. 11, 12 are examples of the metaphase figures in which the observations were carried out. The general aspect of the metaphase rosette as seen in these figures is nothing other than the typical feature of the avian chromosomes, consisting of two distinct size-groups, larger (macro-) and smaller (micro-) chromosomes. The macro-chromosomes occupy the peripheral zone of the equatorial plate, surrounding the micro-chromosomes scattering in the central region (Textfigs. 5-7). After careful counting it was established that the total number of the chromosomes observed in the spermatogonia, so far studied, was 82 (σ , $2n$) with no exception. There is found no significant difference between the two subspecies above mentioned, either in the chromosome number or in the other morphological details. The diploid number is thus different from those reported by previous authors. The

macro-chromosomes are 18 in number, composing 9 pair (*a*'s-*h*'s and *b*'s in Textfig. 5-7). Detailed morphological analysis of these



Textfigs. 5-14. Chromosomes of *Phasianus colchicus* (♂ and ♀). ×4000. 5-6. Spermatogonial metaphases of *Phasianus colchicus karpowi*. 7. Spermatogonial metaphase of *Phasianus colchicus versicolor*. 8-11. Primary spermatocyte metaphases of *Phasianus colchicus karpowi*. 12-13. Oogonial metaphases of *Phasianus colchicus karpowi*. 14. Oogonial metaphase of *Phasianus colchicus versicolor*.

chromosomes indicates that the macro-chromosome complex consists of a pair of the largest V-shaped ones, three pairs of telomitic rod-shaped ones tapering at their inner terminals, a pair of small V-shaped ones having nearly median attachment, and the remaining four pairs of telomitic elements. The serial alignment of chromosomes as shown in Textfigs. 24, 25, 28 will illustrate more clearly than any verbal descriptions. The micro-chromosomes are all telomitic in nature, varying from short rod to minute spheroid as occurred in the Domestic fowl, but the number was found to be 64, instead of 62 occurred in the Domestic fowl. In comparison with the chromosome complement of the Domestic fowl it is quite conspicuous that the number of V-shaped elements is reduced into 2 pairs in the pheasant.

Spermatocyte chromosomes. In order to make the chromosome number observed in the spermatogonial cells more accurate, the haploid number was examined in the primary spermatocyte in the adult testes of the Korean Ring-necked Pheasant, *Phasianus colchicus karpowi*, one of the subspecies used in the present hybridization experiment. With certainty 41 distinct bivalent chromosomes are observable, which have been derived by conjugation of 82 univalent chromosomes, in the central space. The largest element is quite conspicuous in assuming the atelomitic V-shape (Pl. XXV, fig. 13). From this study there seems no slightest doubt to conclude that the chromosome number of the pheasant is 82 in diploid and 41 in haploid.

Oogonial chromosomes. Oogonial chromosomes were studied in the dividing figures of the oogonial cells which were observed in the embryonal ovaries of the Korean Ring-necked Pheasant, *Phasianus colchicus karpowi* and the Japanese Green Pheasant, *Phasianus colchicus versicolor* (Pl. XXV, fig. 14). The general aspect of the complex and the morphology of the individual chromosomes show apparently no difference from those of the spermatogonium, but a close observation reveals that the number of macro-chromosomes is 17 in the oogonium, whereas it is 18 in the male cell. From this the total number of the oogonial complex is found to be 81, one fewer than that of the spermatogonial complement. This numerical difference depends, as in the case of the Domestic fowl, on the fact that the fifth largest V-shaped chromosomes (labelled *e* in Textfigs. 12-14) has no homologous partner in the

female cell, as obviously recognizable by reference to the serial alignment of chromosomes shown in Textfigs. 26, 27, 29. In other words, the small V-shaped chromosome *e* remains always unpaired having no mate of corresponding size in the female complex, while it is present in a paired condition in the male. This fact can be accepted only by assuming the chromosome *e* as the sex-chromosome. Thus, the results of the present investigation agree with those made by Sokolov, Tiniakow & Trofimov ('36) and Suzuki ('39) in respect to the sex-chromosome.

(c) Morphological comparison of the chromosomes between
the Domestic fowl, *Gallus gallus* var. *domesticus*
and the Common Pheasant, *Phasianus colchicus*

The morphological comparison of the chromosomes between the Domestic fowl and the Common Pheasant was chiefly made in the macro-chromosomes referring to their shape and size, since they are distinctly characterised and easy to compare. The micro-chromosomes are rather difficult to compare between the two forms, because they have no distinct characteristic feature.

The morphological analysis of the macro-chromosomes of the Domestic fowl was made by Oguma ('38) in detail and his results quite agree in every point with those obtained in the present study. Furthermore, it became evident now that there exists no racial difference in the chromosomes of the fowl as already noted.

The morphology of the large-sized chromosomes was studied by Sokolov, Tiniakow & Trofimov ('36) and Suzuki ('39), and the results obtained by them seem to show a considerable agreement with those secured in the present investigation. Our observation could not reveal any distinguishable difference in the chromosomes between the two subspecies, *Phasianus colchicus karpowi* and *Phasianus colchicus versicolor*, and also among these and *Phasianus colchicus colchicus* which was studied by Sokolov, Tiniakow & Trofimov ('36).

The comparison of the macro-chromosomes between the Domestic fowl and the Common Pheasant now comes under consideration by reference to the serial alignments of chromosomes shown in Textfigs. 18-23 and 24-29. The first largest pair (*a*'s), apparently showing no difference in both forms, consists of submedian V-shaped elements. A remarkable difference is seen in the chromosome pair of the second rank (*b*'s); in the fowl they are submedian in attach-

ment, while in the pheasant they are telomitic rod-shape. It is noticeable that the latter rod-shaped *b*-chromosomes in the pheasant correspond in length to the long arms of the atelomitic *b*-chromosomes in the fowl. The third largest elements (*c*'s) do not differ between the two forms, being long telomitic chromosomes. There is found again a noticeable difference in the fourth largest chromosomes (*d*'s); in the fowl they are represented by the J-shaped elements having subterminal attachment, whereas they are straight rod-shape in the pheasant, and their length are similar to the long arms of the *d*'s in the fowl. The fifth largest elements (*e*'s) are the sex-chromosomes and quite identical in shape and size in both forms compared, showing the nearly median attachment. The sixth elements (*f*'s) are also indistinguishable from each other, being straight rod-shape of median size. In addition to these elements, there are contained two outstanding chromosomes of telomitic nature in the complex of the pheasant (*b*'s) which are a little shorter than the *f*-chromosomes. The corresponding chromosomes is never present in the fowl. However, it is interesting and important to know that these chromosomes fairly correspond in their length to the short arms of the *b*-elements in the fowl. By the morphological analysis of chromosomes and their comparison thus made, the chromosomal relation between the Domestic fowl and the Common Pheasant may be illustrated as follows: if the detachment between the long and short arms in the *b*- and *d*-chromosomes of the fowl is assumed to occur resulting the production of long and short rod-elements respectively, it will be possible to suppose the appearance of the chromosome complex of the pheasant with four chromosomes in excess. As a matter of fact, the *b*-elements in the pheasant correspond to the long arms of the *b*'s in the fowl and the short arms of the latter are found as *b*'-elements in the pheasant. Moreover, the *d*-chromosomes of the pheasant are also identical with the long arms of *d*'s in the fowl, and the short arms of the latter may be contained in the group of the micro-chromosomes of the pheasant (cf. Textfig. 34). According to these changes, the number of macro-chromosomes increases to 18 (♂) and 17 (♀) in the pheasant instead of 16 (♂) and 15 (♀) in the fowl, and that of the micro-chromosomes of the pheasant becomes two excess than that of the fowl, being 64 in the former and 62 in the latter. In total four chromosomes are present in excess in the pheasant compared with the fowl. A similar ex-

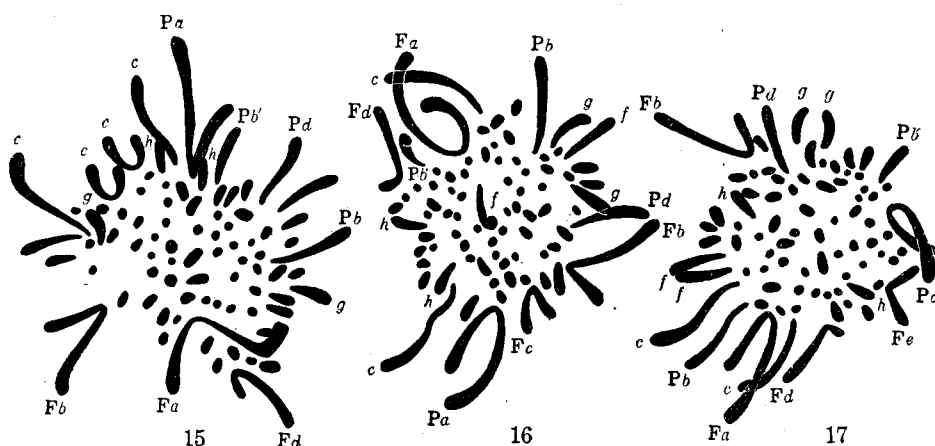
planation has preliminarily been applied by Trofimov & Tiniakow ('33) in the comparison of the karyotypes of the pheasant and the fowl, though their statement was not conclusive at all as they failed to determine the total number of chromosomes in the both forms. According to Tiniakow ('34), an analogous relationship of the chromosomes seems to exist also between the pheasant (*Phasianus*) and the peacock (*Pavo*). The chromosomal relation of a similar type is not rare among the related forms of other vertebrates, and has been reported to exist between the allied species of fishes (Makino '41), urodelan amphibians (Makino '32, '35) and lizards (Matthey '39).

(d) Chromosomes of the hybrid between the Domestic fowl, *Gallus gallus* var. *domesticus* and the Common Pheasant, *Phasianus colchicus*

The chromosomes of the hybrid between the Domestic fowl and the Pheasant has once been studied by Cutler ('18), who entirely failed to draw any accurate evidence due to the technical difficulties, but reporting 18-20 chromosomes in the spermatogonial division. Beside him, there is no reference in the literature which deals with the chromosomes of this hybrid. In the present study, the morphological analysis of the chromosomes in the hybrid and their behaviour was investigated in detail with sufficient material, result of which constitutes the data of the following descriptions.

Spermatogonial chromosomes. Fortunately a number of metaphase figures of spermatogonial division were obtained in the testes of 11-13 days embryos coming from the cross between the Shamo and the Korean Ring-necked Pheasant, example thereof being indicated in Textfig. 15. At a glance the general aspect of the chromosome garniture of the hybrid cell, assuming a typical avian form, seems not differing from those of the parental forms. The complement consists of two distinct size-groups of larger (macro-) and smaller (micro-) chromosomes, the former occupying the peripheral zone of the equatorial plate as usual and enclosing those of smaller size scattering in the central region. Careful examinations reveal that the spermatogonial complex consists of 80 chromosomes, the number being different from either of the parental species, the Domestic fowl and the pheasant. The chromosome constitution is also of quite characteristic. The elements consisting

of the macro-chromosome group are arranged in order of size as follows; a pair of large V-shaped chromosomes of nearly equal size, a little smaller V-shaped chromosome, two long, but nearly equal straight rod-shaped chromosomes, a little shorter rod-shaped chromosome, a J-shaped element of subterminal attachment, a rod-element of median length, a pair of small V-shaped chromosomes of similar shape corresponding to the *e*-chromosomes of the parental species, and three pairs of short rod-shaped chromosomes, and in



Textfigs. 15-17. Chromosomes of the hybrid, *Gallus gallus* var. *domesticus* (the Shamo) × *Phasianus colchicus karpowi* (♂ and ♀). ×4000. 15. Spermatogonial metaphase. 16-17. Oogonial metaphases. F: Chromosomes from the Domestic fowl (*Gallus*). P: Chromosomes from the Pheasant (*Phasianus*).

addition a single rod-shaped chromosome slightly shorter than the sixth largest chromosomes (*f*'s) in length, which is difficult to be sorted out from any other chromosome. It is beyond doubt that the last mentioned, small rod-shaped chromosome is not other than the *b'*-element derived from the pheasant, which is absent in the fowl. As a result, the number of macro-chromosomes becomes 17, an odd number, and accordingly the micro-chromosomes are 63 showing also the odd number (Textfig. 15). Detailed accounts on the morphological analysis of the hybrid chromosomes are given in the latter section.

Oogonial chromosomes. Oogonial chromosomes were studied in germ-cells contained in the developing ovaries of 11-13 days old

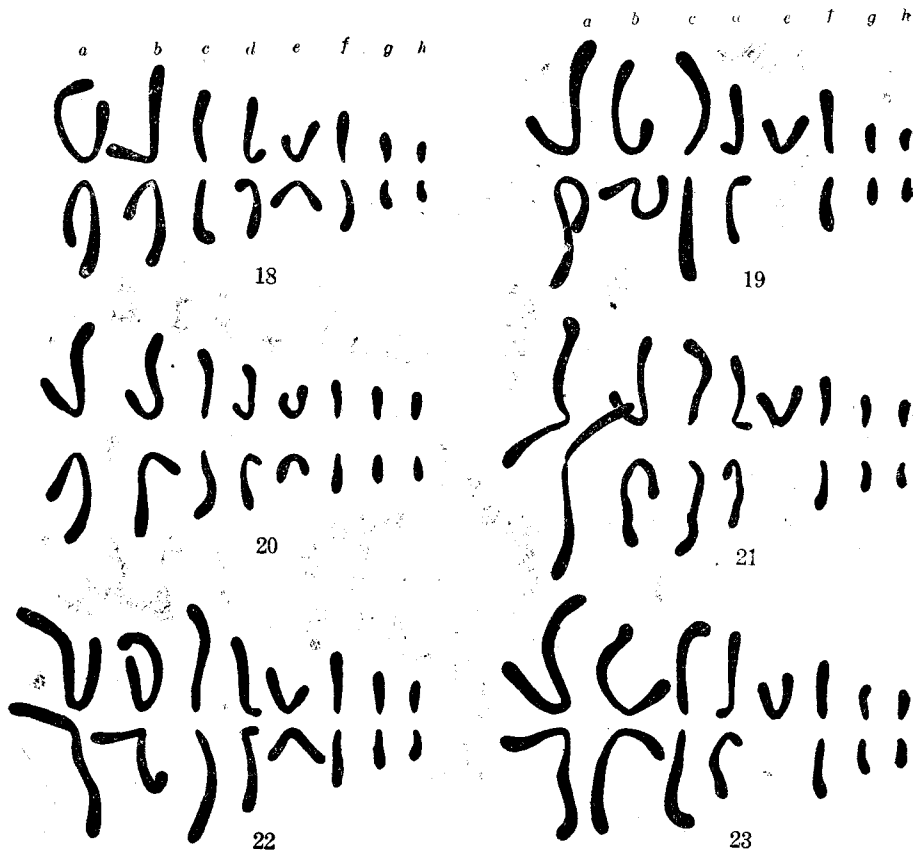
embryos. The general morphological feature of the chromosomes in the oogonial complex bears no apparent difference from those of the spermatogonium. The number of chromosomes contained was decided to be 79 by close examinations of several adequate equatorial plates (Textfig. 16-17). The number is thus one fewer than in the male cells. Close investigations reveal that this numerical difference by sexes is due to the fact that small V-shaped chromosome ranging to the fifth largest in size is present in the unpaired condition in the oogonial cell, while it has a corresponding mate in the male. In the light of this finding, it is quite evident that the fifth largest V-shaped element, namely the *e*-chromosomes, represents the sex-chromosome in the hybrid, same as in the parental forms.

Meiosis in the adult testis. As already pointed out, the auxocytes in the adult testis of the hybrid do not advance in development beyond pachytene stage, and the cells thereafter undergo degeneration. The meiotic division is therefore entirely absent and no gametes are produced. The degeneration of the germinal elements which leads to sterility of this hybrid thus takes place during very early stages of the meiotic process failing to form the meiotic chromosomes.

(e) Morphological analysis of the hybrid chromosomes

For the morphological analysis of the chromosomes in the hybrid and their comparison with the parental forms, the alignmental arrangements of the chromosomes as shown in Textfigs. 30-33 are prepared. After careful analysis of the morphological characters of chromosomes it was accessible that the chromosome elements of the hybrid are derived into two distinct groups having corresponding shape and size. By referring Textfig. 34 it is not difficult to understand that those arranged in the upper row are nothing other than the half set of chromosomes which were contained in the gamete of the Domestic fowl, as clearly recognizable by comparison of the characteristic features of the individual elements with those of the Domestic fowl (cf. Textfigs. 18-23), and also those found in the lower row are to be the half set of chromosomes coming from the gamete of the Common Pheasant, as is clear by direct comparison with the chromosomes of the Common Pheasant (cf. Textfigs. 24-29). In other words, the chromosome complex of the hybrid between the

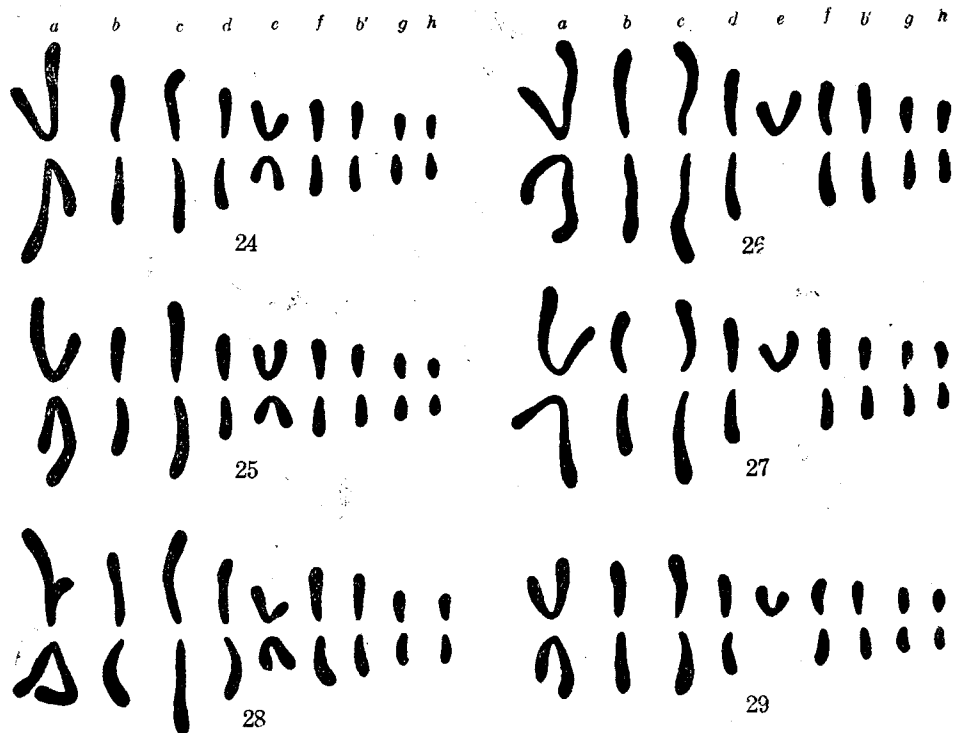
Domestic fowl (σ) and the Common Pheasant (φ) consists of the half set of the chromosomes derived from the cock fowl and the half set of the chromosomes from the hen Common Pheasant. Thus it may be established beyond doubt that the hybrid chromo-



Textfigs. 18-23. Serial alignments of macro-chromosomes of *Gallus gallus* var. *domesticus*. $\times 4000$. 18. Spermatogonial chromosomes of the Shamo. 19. Oogonial chromosomes of the same. 20. Spermatogonial chromosomes of the Shamo Bantam. 21. Oogonial chromosomes of the same. 22. Spermatogonial chromosomes of the Chabo. 23. Oogonial chromosomes of the same.

some complement is a total sum of the half sets of the parental complexes; namely, the number of chromosomes in the male hybrid, 80, is resulted from the sum of the haploid number of the Domestic cock, $n = 39$, and that of the hen pheasant, having e -element, $n = 41$,

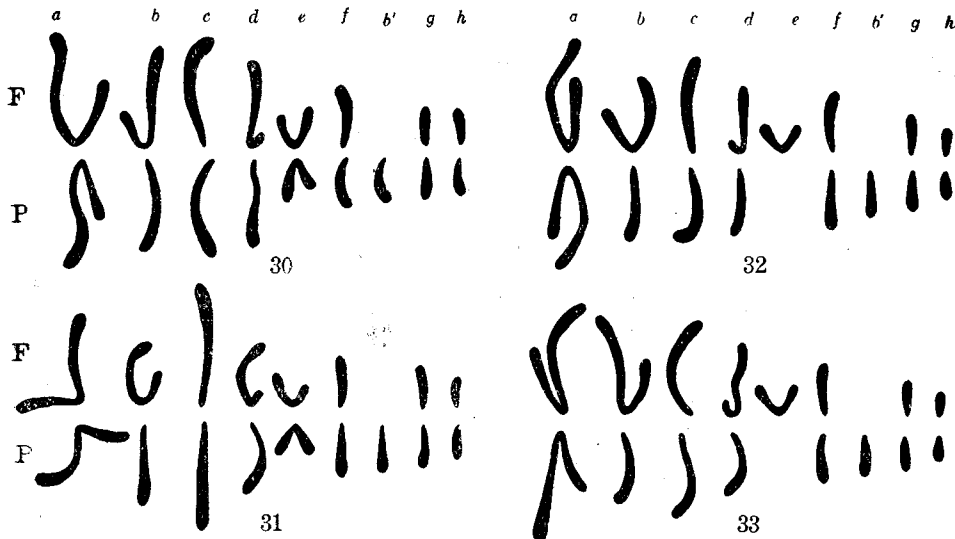
and number of chromosomes of the female hybrid, 79, must be resulted from the sum of the haploid number of the Domestic cock, $n = 39$, and that of the hen pheasant without *e*-element, $n = 40$. It is also noticeable that the parental chromosomes, at least the large elements, can be pointed out in the hybrid complex by the identification of their characteristic features. As already noticed in the fore-



Textfigs. 24-29. Serial alignments of macro-chromosomes of *Phasianus colchicus*. $\times 4000$. 24-25. Spermatogonial chromosomes of *Phasianus colchicus karpowi*. 26-27. Oogonial chromosomes of the same. 28. Spermatogonial chromosomes of *Phasianus colchicus versicolor*. 29. Oogonial chromosomes of the same.

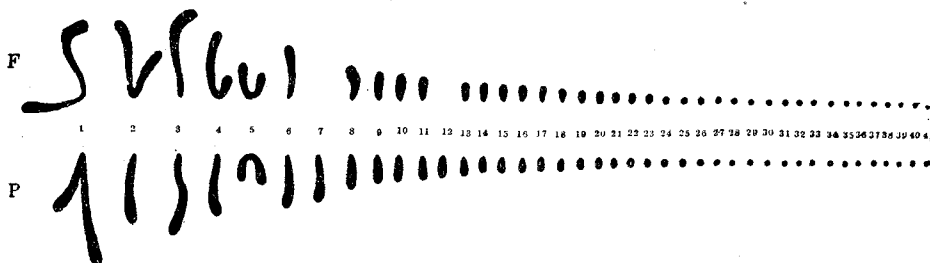
going section, the sexual difference of chromosomes is depended on the fact that the fifth largest V-shaped chromosome, namely the *e*-element, is single in the female cell having no corresponding mate, and it is present in paired condition in the male. It is selfevident that the single *e*-element contained in the oogonial cell is the chromosome which came from the male parent, the Domestic fowl.

In addition to the above material, the hybrids from the reciprocal cross were used in this study for the chromosome observations, the results of which were seemingly identical in every detail with those mentioned above. In this case, however, the *e*-chromosome of the oogonium is derived from the pheasant, not from the Domestic fowl, though it is difficult to distinguish morphologically the *e*-element of the pheasant from that of the fowl.



Textfigs. 30-33. Serial alignments of macro-chromosomes of the hybrid, *Gallus gallus* var. *domesticus* × *Phasianus colchicus karpowi*. × 4000. 30-31. Spermatogonial chromosomes. 32-33. Oogonial chromosomes. F: Chromosomes from the Domestic fowl (*Gallus*). P: Chromosomes from the Pheasant (*Phasianus*).

In order to get more sufficient data of the hybrid chromosomes, some observations were made upon the chromosomes in some somatic cells. Textfigs. 35, 36 are larger chromosomes drawn from the metaphase plates of the epithelial cells of the intestine in the male and female embryo, and Textfig. 37 is those from the nephric cell of a female embryo. Referring these figures, it is evident that the chromosome complex as seen in these embryonal somatic cells of the hybrid shows no difference from those found in the spermatogonial or oogonial cells, as far as our observation is concerned. The fact may be better understood from the serial alignments of these chromosomes as given in Textfigs. 38-40 than verbal description.



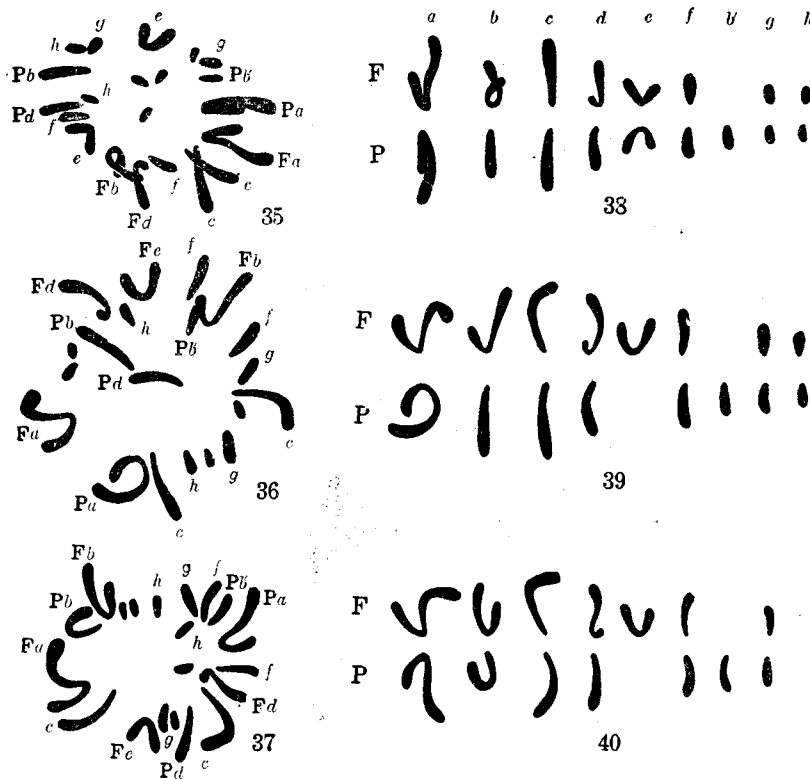
Textfig. 34. Serial alignment of spermatogonial chromosomes (complete set) of the hybrid, *Gallus gallus* var. *domesticus* × *Phasianus colchicus karpowi*. ×3200. F: Chromosomes from the Domestic fowl (*Gallus*). P: Chromosomes from the Pheasant (*Phasianus*).

(3) Behaviour of germ-cells in the F_1 hybrid

The present chapter deals with the behaviour of germ-cells in the F_1 hybrid obtained by various sorts of crosses between the Domestic fowl and the Common Pheasant. The observation indicates that the activity of germ-cells seems to differ in greater or lesser degree depending on the different combination of the cross, but the behaviour of germ-cells closely resembles in each of them examined. Therefore, all cases observed are treated together in the following descriptions.

(a) Spermatogonial and oogonial divisions in the embryonal gonads

The multiplying mitotic divisions of both spermatogonial and oogonial cells proceed quite regularly in the embryonal gonads of the hybrid as in the case of the parental bird, and no abnormality has ever been found in the behaviour of chromosomes either in the spermatogonial or in the oogonial divisions. Figs. 37 and 38 in Pl. XXX are microphotographs taken from a part of the testis of the 11 days embryo, where very active mitotic divisions of spermatogonial cells are recognizable. As already mentioned, the accurate study of chromosomes was made in these dividing cells and the number of chromosomes was determined to be $2n$, 80 in ♂, and $2n$, 79 in ♀ (Textfigs. 15-17).



Textfigs. 35-40. Macro-chromosomes of the somatic cells of the hybrid, *Gallus gallus* var. *domesticus* × *Phasianus colchicus karpowi*. ×3000. 35. From the epithelial cell of intestine of the male. 36. The same, of the female. 37. From the nephric cell of the female. 38. Serial alignment of the macro-chromosomes based on Textfig. 35. 39. The same, based on Textfig. 36. 40. The same, based on Textfig. 37. F: Chromosomes from the Domestic fowl (*Gallus*). P: Chromosomes from the Pheasant (*Phasianus*).

(b) Spermatogonial divisions in the adult testis

It is generally found that the division of spermatogonial cells in the testis of the pure stock of Domestic fowl becomes active with the growth of the bird, and meiotic divisions take place when the bird is close to maturity. Due to the increase of germ-cells the seminal tubules become larger and thicker, until it grows about five to ten times larger in diameter than that of the embryonal stage. In the testis

of hybrid, however, the seminal tubules grow only from two to three times larger in diameter even in the adult bird, and the germ-cells contained in the tubules are very scanty in number. In the majority of tubules only one or sometimes two layers of germ-cells line their inner wall, and most of the germ-cells contained in them are the spermatogonia. In the hybrid of 6 months male in the cross of the Red-hackled Shamo ♂ and *Ph. c. karpowi* ♀ for example, only two or three spermatogonia in process of division were found in ten to twenty tubules observed. As the bird grows older the division of spermatogonia becomes inactive, and in the testis of the male 22 months old the spermatogonial figures in division were hardly found out in the seminal tubules. Even in this inactive testis the chromosome behaviour of the spermatogonia in division is quite regular, and Figs. 39 and 40 in Pl. XXX are taken from the sections of the testis of this 22 months male, in which two or three dividing spermatogonia in the metaphase and anaphase stages are found in the tubules. The chromosome complement observed in this material showed an entire agreement with that presents in the embryonal material. In this respect detailed descriptions are given in the foregoing chapter.

(c) The meiotic phenomena in the adult testis

As referred to the previous sections, the multiplying (mitotic) divisions of the spermatogonial cells take place quite regularly in the adult testes, though not active in division. After several divisions they enter the growing period of the primary spermatocyte. In some material observed, there were found a few cells, in the early growing stage, in the testis of the chick just hatched. But so far observed in this study, the auxocytes were still a few in number in the testes of the 6 months old male. In the testis of the male 10 months old, a little increase of the auxocytes in number is found, and so far as our observations go, the activity of the gonad seems to be highest in this age, but the number of the auxocytes is not so numerous as in the testes of the pure stock of fowl. After detailed study, these auxocytes were proved to be in the leptotene, bouquet, or pachytene stages (Pl. XXX, fig. 41, Pl. XXXI, figs. 42, 43). Not developing beyond pachytene, these auxocytes undergo degeneration, since the cells advanced to diplotene and diakinesis were never found, as far as the present material is concerned (Pl. XXXI, fig. 44).

There are found two distinct types of degeneration of auxocytes in the adult testis. The commonest is that the nucleus begins to shrink in pachytene stage, and at the same time the chromatin elements within it aggregate into masses, undergoing finally pycnotic degeneration. In the other type which occurs rather rarely, the vacuolation of the nucleus takes place in pachytene stage, inside which the chromatic elements dissolve losing staining ability. It is here noticeable that in both cases the Golgi's bodies always appear in these degenerating auxocytes. When the cells completely degenerate they gather in the lumen space of the seminal tubules (Pl. XXXI, figs. 45, 46). These dead cells, however, could not be found in the vas deferens (Pl. XXVI, fig. 19, Pl. XXVII, fig. 23).

As noted above, the auxocytes of the hybrid do not advance beyond the pachytene stage of the growing period and they thereafter undergo degeneration. The meiotic division, therefore, never takes place, consequently no gametes produced in the testis. The degeneration of the germ-cells leading to sterility thus takes place in this hybrid during the quite early stage of the growing period.

(d) Degeneration of the oocytes in the embryonal ovary

Due to insufficient material the behaviour of the oocyte in the ovary was not observed in detail as in the testis, but it is certain in the present observation that the degeneration of the oocytes in the ovary has already been in its course at the time of hatching. By reference to the evidence known in the fowl (Goldsmith '28), the following supposition becomes possible that the degeneration of the oocytes seems to occur early in leptotene stage during the later embryonal stage. For details of the evidence reference may be made to the previous chapter.

(4) Discussion

Considered from the taxonomical relationship, the Domestic fowl, *Gallus gallus* var. *domesticus* and the Common Pheasant, *Phasianus colchicus* are more closely related with each other than between the Muscovy duck, *Cairina moschata* and the Domestic duck, *Anas platyrhynchos* var. *domestica*. But the karyological phenomena revealed by this study indicate that the dissimilarity of the karyo-

type seen in the Domestic fowl and the Common Pheasant is rather great contrasting to that existing between the Muscovy duck and the Domestic duck (Yamashina '41b). The diploid number of chromosomes in the Domestic fowl was determined to be 78 (σ , $2n$) and 77 (φ , $2n$), while that of the Pheasant to be 82 (σ , $2n$) and 81 (φ , $2n$). In addition to this numerical dissimilarity between the two forms, the morphological difference is remarkably shown in the facts that the *b*-chromosome of the Domestic fowl is represented by the V-shaped element, while in the pheasant it is telomitic rod-shape, and that the *d*-chromosome of the Domestic fowl is of J-shape, whereas that of the pheasant assumes rod-shape. As already described in detail, the chromosome complement of the hybrid is quite motley in constitution, due to the union of the parental complexes which contain morphologically dissimilar elements. It cannot be denied that most of these parental chromosomes are not identical in their inner structure. The fact that the structural dissimilarity in the parental chromosomes may be the cause of the failure of pairing at meiosis in the hybrid, has been shown in the author's previous study dealing with the *Cairina* \times *Anas* hybrid (Yamashina '41b). The abnormal meiotic process occurred in the gonad of the *Gallus* \times *Phasianus* hybrid, which leads to sterility of this hybrid, may also be based upon the similar cause as in the *Cairina* \times *Anas* hybrid. The sterility seen in these two cases may be placed under the category of the chromosomal sterility following Dobzhansky ('37). A similar case of hybrid sterility is known to occur in the cross between *Drosophila melanogaster* and *D. simulans*. According to Kerkis ('33) spermatogenesis and oogenesis of *D. melanogaster* \times *D. simulans* hybrid do not advance beyond spermatogonia and oogonia. From the comparative genetical work on *D. melanogaster* and *D. simulans* it has been demonstrated that the arrangement of genes is different in these species, though metaphase chromosomes appear quite identical under the microscope (Sturtevant '29). On the contrary, from the study of the hybrid between race A and race B of *D. pseudoobscura* it was proved that the sterility of this hybrid depends not upon the ultimate source of their cytoplasm (Dobzhansky '36), and that all chromosomes except Y and the fifth one of race A and race B carry genes concerned with the sterility of the inter-racial hybrids (Dobzhansky '36). Based on these evidences Dobzhansky ('37) concluded that the sterility of hybrids in animals

in which gametogenesis is disrupted before meiosis is probably genic.

The fact that the degeneration of the germ-cell occurs in the earlier stage in the *Gallus* × *Phasianus* hybrid than in the *Cairina* × *Anas* hybrid should be considered here. In the matter of fact, the germ-cells undergo degeneration during very early stages of the meiotic process in the case of *Gallus* × *Phasianus* hybrid, during pachytene in the testis and probably in leptotene in the ovary, while in the *Cairina* × *Anas* hybrid, the germ-cells advance to the first meiotic metaphase and then degenerate (cf. Yamashina '41b). It cannot be denied here that one of the important causes lies in the fact that the structural dissimilarity of the chromosomes is much greater between *Gallus* and *Phasianus* than between *Cairina* and *Anas*. Further the relationship existing between the nucleus and the cytoplasm cannot be overlooked in the case of hybrid sterility. In this connection, an important reference is seen to the study on "Melogonischen Amphibienbastarde" published by Boehringer ('38). In this study he arrived the conclusion that the chromosomes display the highest vitality in own cytoplasm, but it becomes lesser in the cytoplasm of different species. Since it is naturally considered that such a relationship also exists in the other animals such as birds, the effect of the nuclear elements (the chromosomes) which came from the Domestic fowl to the cytoplasm derived from the Common Pheasant is to be considered in the cross between the Domestic fowl (♂) and the Common Pheasant (♀). In this case it is probable that the nuclear material of the Domestic fowl becomes inactive when it enters into the egg-cytoplasm of the pheasant, since the cytoplasm of the Common Pheasant is considerably different in its nature from that of the Domestic fowl, the difference being shown, for instance, from the serological investigation by Nakagawa & Sasaki ('41). The effect of the cytoplasm of the one species upon the nucleus of the other species in the hybrid would not act in most case to disturb the vitality in the somatic division, but its ill effect would be displayed in the germ-cells when they enter the meiotic process. Between *Gallus* and *Phasianus* the chromosomal dissimilarity is high, as already noticed, and at the same time the affinity of the nucleus to the foreign cytoplasm is rather weak between them. From these considerations the following conclusion will possibly be gained that, in the case of the *Gallus* × *Phasianus*

hybrid the germ-cells undergo degeneration very early in the meiotic process, such as in leptotene and pachytene. In the hybrid between *Cairina* and *Anas*, the chromosomal dissimilarity is not so great between the two and the nucleus of the one species would have a close affinity to the cytoplasm of the other species. By these reasons, the germ-cells in the *Cairina* × *Anas* hybrid advance to the first meiotic metaphase and thereafter development arrested.

Thus, for the cause of sterility in the hybrid two important factors at least are necessarily to be taken into account: the one is the dissimilarity of the chromosomes in the parental species, and the other is the affinity of the nuclear material of the one species with the cytoplasm of the other species. In the case when the chromosomal dissimilarity is very large between the parental animals and the affinity of the nuclear material of the one species with the cytoplasm of the other species is very weak, the degeneration of the germ-cells occurs very early, without conjugation between the parental chromosomes. According to the combination of these two factors, the degeneration of germ-cell may take place in early or later stages of the meiotic process. An adequate instance in which the chromosomal dissimilarity is extremely small, and, at the same time, the nuclear cytoplasmic relation is intimate between the parental species, will be found in the cross between *Syrnaticus* and *Chrysolophus* which is dealt with in the following part.

Part II. Accounts regarding the hybrids between the Japanese Copper Pheasant, *Syrnaticus soemmerringii* and the Golden Pheasant, *Chrysolophus pictus*

A hybrid obtained from the cross between the Japanese Copper Pheasant, *Syrnaticus soemmerringii* and the Golden Pheasant, *Chrysolophus pictus* seems to be produced for the first time at the aviary of Marquis Nagamichi Kuroda (Tokyo) in 1919, and it lived up to 1930. Recently, Mr. Shunkichi Nomura attempted the mating of the Japanese Copper Pheasant and the Golden Pheasant in his aviary at Tokyo, and in 1940 obtained thirty two F₁ hybrids, of which thirteen were reared up to maturity. By the courtesy of Mr. Nomura, three males and three females were placed at the author's disposal, for which the present investigation was carried out.

This hybrid was thus produced very rarely and no scientific study has been extended on it. The taxonomical relationship between the parental species suggests that the hybrid between them may be incomplete fertile, in the light of the fact that the male hybrid from the mating between *Syrnaticus reevesi* and *Chrysolophus pictus* was known to be incomplete fertile according to the study of Poll ('10).

(1) Anatomical and histological observations on the reproductive organs in the hybrid birds

In the F_1 hybrids sexes are clearly distinguishable by either external character or by plumage (Pl. XXIV, figs. 5, 6). According to Mr. Nomura, the breeder of this hybrid, the number of male and female individuals in F_1 generation is nearly equal, thus no anormous inclination of the sex-ratio seems to occur in this hybrid.

Adult male. The material used here consists of two males hatched in June, 1940 and killed in March and April of 1941 when they are 9 and 10 months old respectively. They are considered to be sexually mature and their testes have grown large, measuring 15×5 mm. in one example, and its size is a little larger as compared with the case of the *Gallus* \times *Phasianus* hybrid in a same age, but much smaller than the organ of the pure Gallinaceous birds. In the microscopical examination the seminal tubules, not so meagre as in the case of the *Gallus* \times *Phasianus* hybrid, are well developed and filled with germ-cells within (Pl. XXXII, fig. 47). Spermatogonia and spermatocytes in the various stages in development were found forming several layers. It is of special interest to see that the complete equatorial plates of the primary and secondary spermatocytes are formed, and also that apparently regular divisions are found in them (Pl. XXXIV, figs. 57-60). The testes of the hybrid are quite evident, in contrast to the testes of birds of pure line, in having numerous deformed spermatozoa and degenerated germ-cells together with seemingly normal spermatozoa. The arrangement of spermatocytes, spermatids and spermatozoa within the seminal tubule becomes irregular to a great extent (Pl. XXXII, figs. 48, 49). When the number of normal spermatozoa, deformed spermatozoa and degenerated germ-cells was examined in an unit area in which the normal spermatozoa are rather numerous, we can find five normal ones for each thirty to forty abnormal ones, hence

it will be possible to state that about 85–90% of germ-cells may undergo degeneration and the remaining 10 to 15% may develop to the spermatozoa which seem to be normal in appearance. Therefore, even if this male hybrid is mated, it may perhaps be quite rare to yield its offsprings.

Adult female. Two females, 10 months and 22 months old respectively, were dissected in their breeding season, and the genital organs were examined compared with those of individuals of pure line. In 10 months old female the ovary, smooth in its appearance, was very small in size as compared with that of the parental specimens, about seven follicles approximately 2 mm. in diameter being found macroscopically on its surface (Pl. XXXII, fig. 50). Fig. 51 is a section of the ovary showing a portion where no follicle is found on the surface, and it is shown that the interstitial tissue and the connective tissue developed to a great extent in the ovary, while the oocytes of normal shape are entirely absent among them, though a few of atrophied follicles being present. The evidence showing that almost all oocytes remaining some incomplete follicles have already undergone degeneration, seems to correspond to the fact that the greater parts of germ-cells in the male have disintegrated in the testis excepting a few which will develop into normal spermatozoa.

Very rudimentary oviduct was found in the normal position, and Pl. XXXIII, fig. 52 depicts the cross section of the oviduct at a portion corresponding to the uterus: its wall is very thin, being only about 2×1 mm. in diameter. Histologically, the oviduct has a quite rudimentary structure, showing incomplete muscle layer and apparent degeneration of gland cells, and only a few epithelial cells possess the cilia. Though the opening out to the fallopian tube was ascertained, general structure of the oviduct clearly shows that this oviduct is not functional (Pl. XXXIII, fig. 53).

The 22 months old female was found to have much more rudimentary ovary than in the former, and in some parts of the ovary abortive degenerating follicles were found in sections (Pl. XXXIII, figs. 54, 55). Though anterior end of the fallopian tube opens normally, the oviduct is quite rudimentary in the histological structure, as seen in Fig. 56. From these evidences it is quite clear that this female is also infecund in sexual reproduction.

(2) *Chromosome studies on the parental species
and their hybrids*

There seems no reference in the literature concerning the chromosomes of the Japanese Copper Pheasant, *Syrnaticus soemmerringii* and the Golden Pheasant, *Chrysolophus pictus*. The chromosomes of these two forms and of the hybrid, closely investigated in the present study, are described in the following paragraphs.

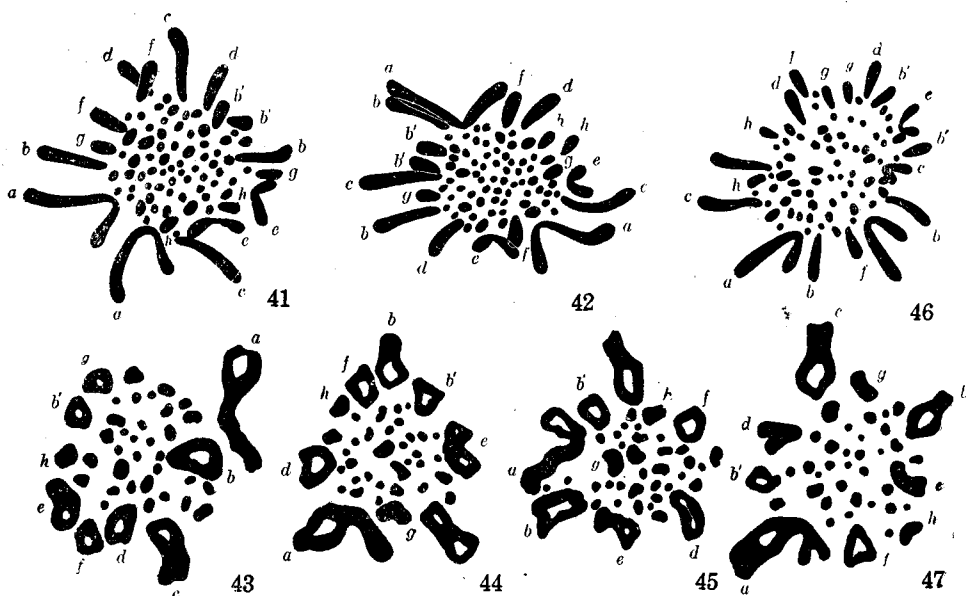
(a) *Chromosomes of the Japanese Copper Pheasant,
Syrnaticus soemmerringii*

Spermatogonial chromosomes. A number of good metaphase figures of the spermatogonial division, available for study, was found in the matured testes of *Syrnaticus soemmerringii scintillans*, two of which are given in Textfigs. 41, 42, where one can easily notice that the karyotype of this species assumes a close resemblance to that of the Common Pheasant. Close comparison, however, detects some differences between these two forms; remarkable difference is shown in the fact that the second chromosomes (*b*'s) are a little longer in *Syrnaticus* than in *Phasianus*.

After careful examination of the metaphase complex it was determined that the diploid number of chromosomes contained in the spermatogonium is 82 ($2n$), showing complete agreement with that observed in *Phasianus colchicus*. As in *Phasianus colchicus* the diploid complement can be sorted into two distinct groups, namely those of the macro- and micro-chromosomes. The macro-chromosomes are 18 in number (*a-h* and *b'* in Textfigs. 41, 42), among which the first and fifth largest pairs are of conspicuous V-shape, as in the case of *Phasianus*. The fifth largest, small V-shaped elements correspond in size and shape to the *e*-chromosome of the Domestic fowl and the pheasant as well. Unfortunately the female chromosomes of this species were not examined at present due to the lack of material, but the similarity of the karyotype to *Phasianus* sufficiently suggests that these fifth largest V-shaped ones are nothing but the sex-chromosome. The evidence is clearly shown by comparison of the serial alignments of chromosomes between this species (Textfigs. 52-54) and *Phasianus* (Textfigs. 24-29). The rest of the macro-chromosomes is of telomitic nature being rod-shaped and tapering at their inner terminals. The micro-chromo-

somes, apparently of telomitic in structure, vary in shape from short rod to minute spheroid in a graded series.

Spermatocyte chromosomes. A number of well fixed metaphase complexes of the primary spermatocytes was observed in the adult testis of the present species and the examples are shown in Textfigs. 43-45. In each plate examined there are always contained 41 distinct bivalent chromosomes which are derived by conjugation of 82 spermatogonial chromosomes. Nine macro-bivalents are quite remarkably arranging in the peripheral zone of the equatorial plates. Though not observed in this study, there is no doubt that as a result of the first division the secondary spermatocyte may possess the same complex of the chromosomes.



Textfigs. 41-45. Chromosomes of *Syrmaticus soemmerringii scintillans* (σ). $\times 4000$. 41-42. Spermatogonial metaphases. 43-45. Primary spermatocyte metaphases.

Textfigs. 46-47. Chromosomes of *Chrysolophus pictus* (σ). $\times 4000$. 46. Spermatogonial metaphase. 47. Primary spermatocyte metaphase.

(b) The chromosomes of the Golden Pheasant,
Chrysolophus pictus

Spermatogonial chromosomes. Spermatogonial chromosomes of this species were investigated in the germ-cells contained in the testes

of 11-13 days old embryos and one of the examples is given in Textfig. 46 which is in the most excellent shape so far examined. Careful counting of the metaphase complex shows that the number of chromosomes was decided to be 82 in total, in full accordance to that of *Syrnaticus* and *Phasianus* already studied. Further, among the 18 macro-chromosomes the first and fifth largest elements are represented by the V-shaped and the remaining pairs telomitic rod-shaped ones. The micro-chromosomes are all telomitic nature and diminish in a graded series. Thus, a close comparison of the corresponding elements of the metaphase complement reveals no apparent difference among the chromosomes of *Syrnaticus*, *Phasianus* and the present species, as far as general configuration is concerned.

Spermatocyte chromosomes. A number of well fixed metaphase complexes of the primary spermatocytes were observed in the adult testis of the present species and an example is shown in Textfig. 47. In each plate examined there are always contained 41 distinct bivalent chromosomes which are derived by conjugation of 82 spermatogonial chromosomes. Nine macro-bivalents are quite remarkable arranging in the peripheral zone of the equatorial plates.

Oogonial chromosomes. Observations were made on the dividing oogonia found in the developing ovaries of 11-13 days old embryos. Comparison of the chromosome complements between the male and female shows that the fifth largest V-shaped chromosome (*e*) has no homologous mate in the female cell as clearly recognizable by means of serial alignments of chromosomes (Textfigs. 57, 58). Namely, the chromosome *e* remains always unpaired in the female complement, while it is in a paired condition in the male. This fact can be understood only by assuming the fifth largest element to be the sex-chromosome, because the presence of this element causes the sexual difference of chromosomes.

- (c) Morphological comparison of the chromosomes between the Japanese Copper Pheasant, *Syrnaticus soemmerringii* and the Golden Pheasant, *Chrysolophus pictus*

As mentioned above, the general aspects of the chromosomes are quite identical between *Syrnaticus* and *Chrysolophus*, but a close analysis of the morphological feature by way of comparison between

each corresponding chromosome points out a slight but clear difference in the second largest, *b*-chromosome, and no other visible difference among other elements is visible. That is, the length of the *b*-chromosome is not identical between the two species. For the purpose of comparison, the ratio of length between the *b*'s and *c*'s was calculated in each species, since the *c*-pair is fairly equal in length in both species. In the following table the value of the ratio obtained is indicated, together with the data obtained in *Phasianus*.

Table 3

Ratio of length between *b*'s and *c*'s

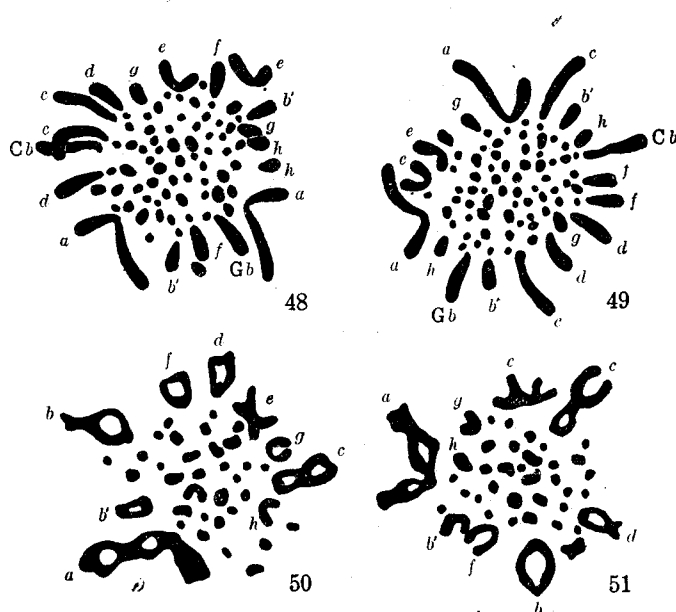
Species	Ratio of <i>b/c</i>
<i>Syrnaticus soemmerringii</i>	0.79
<i>Phasianus colchicus</i>	0.77
<i>Chrysolophus pictus</i>	0.68

From the data, it is evident that the ratio in length thus obtained between the *b*'s and *c*'s is quite appreciable and serves as a basis for specific distinction in each species. Further, the ratio of the length in the *b*-elements between the Copper Pheasant and the Golden Pheasant was obtained to be 0.86.

- (d) The chromosomes of the hybrid between the Japanese Copper Pheasant, *Syrnaticus soemmerringii* and the Golden Pheasant, *Chrysolophus pictus*

The chromosomes of the hybrid birds herein dealt with were studied in the germ-cells from the adult testes.

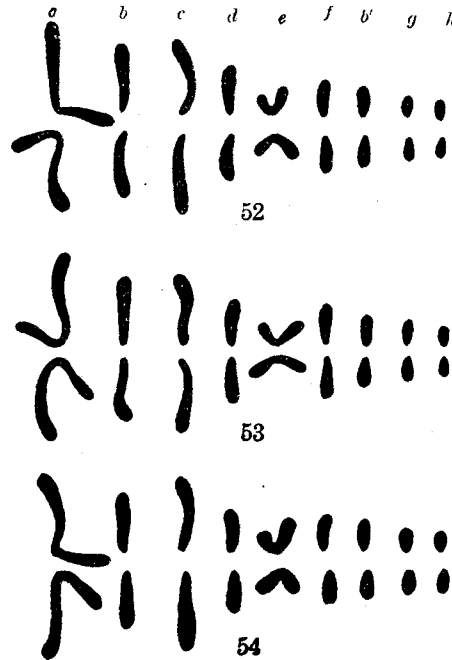
Spermatogonial chromosomes. A sufficient number of metaphase plates was examined and it was found that the spermatogonium contains 82 chromosomes, showing the same number as the parental species. The general aspect of the complements is also indistinguishable from that of the parental species. As in the case of parental birds, the complex clearly shows two distinct size-groups, macro- and micro-chromosomes. The first and fifth largest chromosomes among the macro-chromosomes are of V-shape, the others being telomitic elements. The macro-chromosomes occupy the peripheral zone of the equatorial plate, and surround the micro-chromosomes scattering in the central region (Textfigs. 48, 49).



Textfigs. 48-51. Chromosomes of the hybrid, *Syrmaticus soemmerringii scintillans* × *Chrysolophus pictus*. ×4000. 48-49. Spermatogonial metaphases. 50-51. Primary spermatocyte metaphases. Cb: the b-chromosome from the Japanese Copper Pheasant (*Syrmaticus*). Gb: the b-chromosome from the Golden Pheasant (*Chrysolophus*).

Since the female chromosomes were not studied due to the lack of material, the direct identification of the sex-chromosome was not made in this investigation. Having considered from the conditions existing in the parental forms, however, it is beyond doubt that the sex-chromosome will be represented by the fifth largest V-shaped chromosome (Textfigs. 59-62).

Spermatocyte chromosomes. It is interesting to see that in this hybrid testis the primary spermatocytes form complete metaphase equatorial plates and divide in regular manner. In the metaphase plate of the primary spermatocyte there are contained 41 distinct chromosomes of bivalent nature (Textfigs. 50, 51). That is, this haploid number corresponds to the reduced number of the parental species. It seems to be evident from this fact, that the corresponding elements of the parental chromosomes completely conjugate and form the bivalent chromosomes in meiosis. The general aspect of the metaphase chromosomes in the first division shows no visible

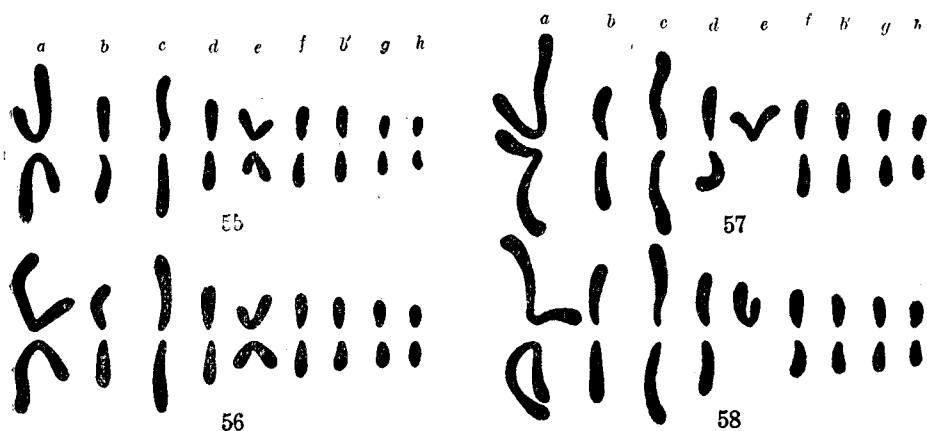


Textfigs. 52-54. Serial alignments of spermatogonial macro-chromosomes of *Syrmaticus soemmerringii scintillans*. $\times 4000$.

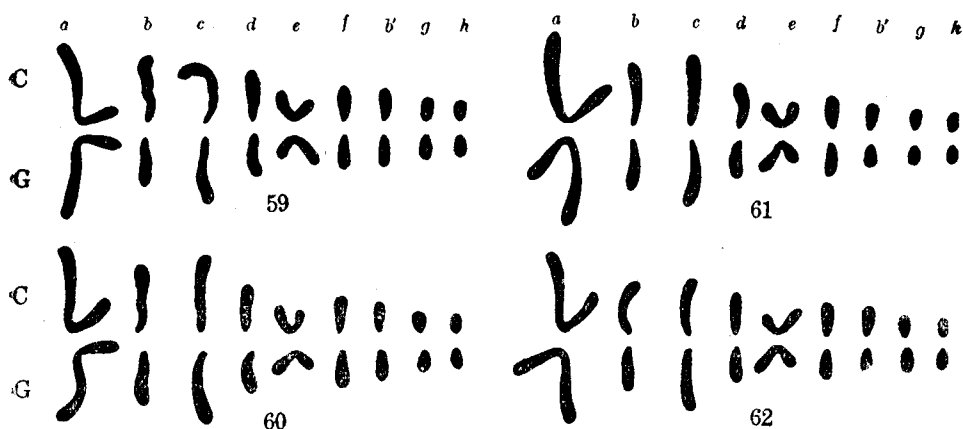
difference from that observed in *Syrmaticus soemmerringii*, one of the parents.

(e) Morphological analysis of the hybrid chromosomes

As noted in the foregoing descriptions, the remarkable visible difference of the chromosomes between the parental forms, *Syrmaticus soemmerringii* and *Chrysolophus pictus*, lies in the length of the second largest, *b*-chromosome. This size-difference of the *b*-chromosome existing in the parents is quite clearly found also in the hybrid complex. That is, the length of two corresponding *b*-chromosomes in the diploid complement is not equal in the hybrid cells. In a number of cells, the ratio of the length between the *b*-chromosomes was measured, and an average value was obtained to be 0.81 (Textfigs. 63-66), which is quite similar to that already calculated in the parental forms (p. 350). On the basis of this fact it is self-



Textfigs. 55-58. Serial alignments of macro-chromosomes of *Chrysolophus pictus*. $\times 4000$. 55-56. Spermatogonial chromosomes. 57-58. Oogonial chromosomes.

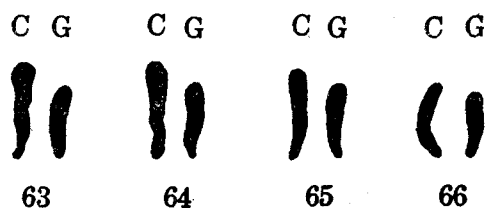


Textfigs. 59-62. Serial alignments of spermatogonial macro-chromosomes of the hybrid, *Symaticus soemmerringii scintillans* \times *Chrysolophus pictus*. $\times 4000$. C: Chromosomes from the Japanese Copper Pheasant (*Symaticus*). G: Chromosomes from the Golden Pheasant (*Chrysolophus*).

evident that the long *b*-chromosome in the hybrid complement, labelled *Cb* in figures, was derived from the Japanese Copper Pheasant, *Symaticus soemmerringii* and the short *b*-chromosome, labelled *Gb*, came from the Golden Pheasant, *Chrysolophus pictus* (Textfigs. 48, 49).

(3) Behaviour of germ-cells in the F₁ hybrid

In regard to the chromosomes of the hybrid dealt with here, detailed descriptions were made in the foregoing sections, and the behaviour and division of the germ-cells may be concerned in the present section.



Textfigs. 63-66. Showing the *b*-chromosome pairs found in the spermatogonia of the hybrid, *Syrnaticus soemmerringii scintillans* × *Chrysolophus pictus*. ×5600. C: Chromosome from the Japanese Copper Pheasant (*Syrnaticus*). G: Chromosome from the Golden Pheasant (*Chrysolophus*).

(a) Spermatogonial division in the adult testis

As in the cases of the hybrids, *Gallus* × *Phasianus* and *Cairina* × *Anas*, already studied, the multiplying division of spermatogonial cell was also normal in the present material. The separation of every chromosome was carried on in quite regular way as occurs in the parental species. Differing from the case of the *Gallus* × *Phasianus* hybrid, the spermatogonial division seems to be active in this case, the cells under active division being found in various parts of the testis. Thus, by the repeated divisions the number of the spermatogonial cells is multiplied (Pl. XXXIV, fig. 57).

(b) The first meiotic division

Following the multiplying divisions the spermatogonia pass into the growing period of meiosis, during which the auxocytes undergo a marked growth. The nuclear phenomena traced through the stages of the growing period, leptotene, bouquet, pachytene, diplotene and diakinesis, are found to be entirely regular by general survey, being not different from those occurred in the parental specimens (Pl. XXXIV, fig. 58). Thus, the meiotic prophase of this

hybrid seems to follow the regular course of changes and the complete bivalents are formed in the following metaphase (Pl. XXXIV, figs. 59, 60). In fact, the number of chromosomes found in the primary spermatocyte metaphase was constantly half the diploid number obtained in the spermatogonial cell of this hybrid, so far as the scope of the present observations is concerned. Hence it cannot be denied to conclude here that every homologous chromosomes coming from two parents regularly conjugate with each other and transform into complete tetrads (bivalents). The tetrads thus



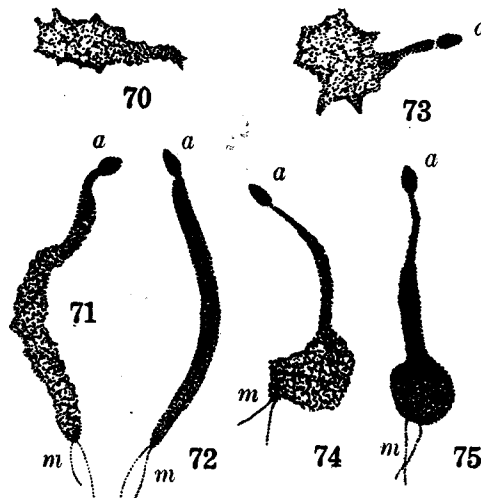
Textfigs. 67-69. The first meiotic divisions found in the testis of the hybrid, *Syrnaticus soemmerringii scintillans* × *Chrysolophus pictus*. The segregation of bivalents normally takes place. ×4000. 67. Early anaphase. 68. Late anaphase. 69. Telophase.

formed are found to be separated each into daughter halves in the first division, in the regular manner (Textfigs. 67-69), and as a result two daughter cells, the second spermatocytes, are produced. The majority of the primary spermatocytes thus produce the secondary spermatocytes. Together with these secondary spermatocytes, there are contained in the seminal tubules a certain number of germ-cells under the process of degeneration, which are difficult to find in the testes of parental birds. This evidence seems to show that the degeneration has occurred in some of the primary or secondary spermatocytes, in this respect mentions may be made later (p. 358).

(c) The second division

The secondary spermatocyte chromosomes, resulted from the first meiotic division, form the metaphase plate of the second division

in most cases. The chromosomes are apparently regular in the equatorial plate, and divide in anaphase each into two daughter elements, following to the regular course. Thus, in most cases, there are produced two daughter cells, the spermatids. In contrast to the above case, some of the secondary spermatocytes undergo degeneration before the division of the cytoplasm has taken place; as a result they appear as the binucleate spermatids (Pl. XXXV, figs. 62-64). The greater parts of germ-cells, however, yield the spermatids with normal appearance as above mentioned; they follow



Textfigs. 70-72. Normal features of spermioteleosis found in the testis of the hybrid, *Syrmaticus soemmerringii scintillans* × *Chrysolophus pictus*. ×4000. a: acrosome, m: middle piece.

Textfigs. 73-75. Abnormal features of spermioteleosis found in the same hybrid. ×4000. a: acrosome, m: middle piece.

later on the course of spermioteleosis; the nucleus elongates into a rod-shape, with the acrosome at its tip. Thus, some of them are transformed into seemingly normal spermatozoa, though quite scanty in number (Pl. XXXII, fig. 48). In most of the spermatids the nucleus does not elongate into an usual spindle shape, as in the normal one (Textfigs. 70-72), but exhibits quite irregular transformation leading to a monstrous feature (Textfigs. 73-75). At first, a part of the chromatic material contained in the nucleus begins to elongate into rod-shape having an acrosome body at the

top, while the rest of the chromatic material forms an irregular chromatic clump. Then the rod-shaped part elongates further into the body like the distal portion of a normal spermatozoon. The middle piece coming from the centrosome appears to attach at the proximal region of the irregular chromatic clump, which then transforms into a compact spherical body. During these changes the cytoplasm is cast off and there appear abnormal spermatozoa having the appearance of a tad-pole. Pl. XXXV, figs. 65-67 illustrate the process of the transformation as above mentioned. Beside these abnormal spermatozoa, there are observed unusual spermatids containing the chromatic body constricted off into two hemispheres, accompanied by a rod-shaped body (Pl. XXXV, fig. 64).

(4) Discussion

The karyological phenomena observed in the hybrid, *Syrmaticus soemmerringii* × *Chrysolophus pictus*, are markedly different in the several important points from those found in *Cairina* × *Anas* and *Gallus* × *Phasianus*. On these points some considerations will be made below.

As already shown, the morphological observation of the chromosomes of the parental species, *Syrmaticus* and *Chrysolophus*, evidences that the chromosomes are nearly identical in their external characters between the two, excepting the *b*-elements which are slightly different in their length. In spite of this difference in the *b*-chromosomes, the latter conjugate and form a complete bivalent in the meiotic division of the hybrid between these two species. This evidence is quite contrast to the phenomenon observed in the *Cairina* × *Anas* hybrid. That is, the *a*-chromosome is nearly equal in its morphological character between *Cairina* and *Anas*, but in the hybrid between the two forms, the *a*-chromosomes do not conjugate in meiosis and remain as univalents (cf. Yamashina '41b). The explanation of these phenomena will be as follows: the *b*-chromosomes of *Syrmaticus* must be similar in the most part of its inner structure to that of *Chrysolophus*, although there is present a size difference between them, and therefore, they conjugate in meiosis of the hybrid; the *a*-chromosomes of *Cairina* and *Anas* are structurally dissimilar in spite of their external similarity in shape and size, and due to this structural dissimilarity the *a*-chromosomes

fail to conjugate in the meiosis of the latter hybrid. As the exceptional case some of the spermatocytes undergo degeneration during the meiotic process in the hybrid testis as already described. On this point an explanation will be made in the following. The chromosomes of *Syrmaticus* and *Chrysolophus* are nearly identical with each other in the external character. Strictly speaking, however, the chromosomes of *Syrmaticus* would not be exactly the same in their inner structure as those of *Chrysolophus*, and some differences, though slight, would be present between each corresponding chromosomes. Since the difference of chromosomes is not so great between *Syrmaticus* and *Chrysolophus*, as in the case between *Cairina* and *Anas*, the chromosomes are able to come to conjugation at meiotic metaphase of the hybrid between *Syrmaticus* and *Chrysolophus* when the condition is favourable, as the case encountered in the foregoing observations. But in unfavourable condition, where, for instance, the corresponding chromosomes occupy the situation quite inconvenient to pair with each other, there would possibly occur the failure of pairing in some chromosomes. In this case, the degeneration may occur in the stage of the primary spermatocyte, as in the case of *Cairina* \times *Anas*. However, in the case when the first meiotic division carries on, the formation of some abnormal secondary spermatocytes may be possible to occur, because of incomplete separation of chromosomes due to their abnormal pairing. In this case, it may be possible to think that about a half of the secondary spermatocytes would undergo degeneration due to unusual amount of the chromosomes contained, while the other half may advance to the metaphase stage and produce spermatids by division. If the half of the spermatids thus formed possess the abnormal chromosome contents, they degenerate either in the early stage of spermioteleosis or develop into the monstrous spermatozoa. And thus, the germ-cells which develop into spermatozoa having normal external feature were found to be 10 to 15% in all as shown in the foregoing observations.

In any species of animals, so far as the author is aware, there has never been reported a similar example as the present case in which the cause of sterility lies in the abnormality of spermioteleosis with the reduction division being normally carried. Dobzhansky ('34) reported a case of sterility existing in the interracial hybrid between race A and race B of *Drosophila pseudoobscura*, in which

the conjugation of the homologous chromosomes of the hybrid is complete, but in the first division the spindle elongates enormously and bends into a ring, and the cell body fails to divide. Consequently, the second meiotic division is absent, and giant binucleate spermatids thus formed degenerate. According to him, the cytoplasm does not concern with sterility in this case, but it is due to genes numbering at least eight. That is, the sterility of the race A \times race B hybrid in *D. pseudoobscura* is resulted by the genes; the genic sterility. It is evident, therefore, the present case (*Syrnaticus* \times *Chrysolophus*) is not comparable in the cause of sterility with the condition found in the interracial hybrid of *D. pseudoobscura*. So far as the observations go, it can be stated with certainty that the sterility in the hybrid *Syrnaticus* and *Chrysolophus* is not due to the action of gene or genes which deals with the sterility. The degeneration of germ-cells and the formation of abnormal spermatozoa as occurred in the testis of the *Syrnaticus* \times *Chrysolophus* hybrid, which lead to sterility of this organism, are possibly produced by the chromosomal cause on the one hand, and on the other hand by the interrelation between the nucleus and cytoplasm derived from the different species. Detailed considerations on this respect may be made later.

Hybrid sterility established in the intergeneric cross is known to occur in the hybrid between the Domestic cow (*Bos taurus*) and the yak (*Poephagus grunniens*), and also between the horse (*Equus caballus*) and the ass (*Equus asinus*). Though no accurate studies have been made on their germ-cells, these hybrids seem to be of comparable with the present case in the nature of sterility.

In plants many comparable cases are known; for example, the hybrid from the crosses *Ribes sanguineus* \times *R. aureum* (Tischler '06), *Digitalis lanata* \times *D. micrantha*, *D. purpurea* \times *D. ambigua* (Haase-Bessell '21), *Epilobium montanum* \times *E. hirsutum* (Håkansson '34), *Pisum humile* \times *P. sativum* (Lutkow '30), *Lobium perenne* \times *Festuca pratensis* (Peto '33) are all sterile. But detailed investigations of their germ-cells have never been carried on, and no clear-cut interpretation has been made for the cause of sterility. Recently Morinaga ('39) reported that the hybrid between Japanese and Indian forms of *Oryza sativa* produces sterile offspring in about 50%, and he explained this phenomenon by the segmental interchange. According to Michaelis ('33) the hybrid between *Epilobium*

hirsutum ♀ and *E. luteum* ♂ was total sterile, while the reciprocal hybrid is fertile. When being back crossed the latter with *hirsutum* ♂, even in F₈ generation the hybrid shows fertility, and after analysis of phenomena he arrived at a conclusion that the results obtained can be explained by assuming cytoplasmic inheritance which suppresses the fertility. In the case of the hybrid of birds the effect of maternal inheritance cannot be accepted as the cause of sterility, since there is no positive evidence at the present. Thus, the explanations maintained by Morinaga ('39) and Michaelis ('33), mentioned above, are not applicable for the illustration of the cause of sterility of the present *Syrmaticus* × *Chrysolophus* hybrid.

As stated before, in the hybrid of *Syrmaticus* × *Chrysolophus*, the conjugation of chromosomes was seemingly normal in meiosis and the meiotic divisions were carried on in quite regular manner, and abnormality which leads to sterility of this hybrid occurs in most cases during or after the second division. The cause by which such later stages of meiosis are lead to disturbance lies, at least in the author's knowledge, in two factors: the one is the chromosomal dissimilarity and the other is the interrelation between the paternal nucleus and the maternal cytoplasm, as in the case of the *Gallus* × *Phasianus* hybrid. As shown in the foregoing description, the chromosomes of the parental forms, *Syrmaticus* and *Chrysolophus* are quite similar in their external feature. But the similarity of the chromosomes as seen at the metaphase stage is not necessarily proportional to the similarity of their inner structure, as clearly demonstrated in *Drosophila melanogaster* and *D. simulans* (Sturtevant '20-21, '29). It is most probable that, though the apparent identity of the metaphase configurations is seen between *Syrmaticus* and *Chrysolophus*, invisible differences may be present in their inner structure between the chromosomes of these two species. The difference in the inner structure, however, would be much less greater between these two, than the relation existing between *Gallus* and *Phasianus* and that between *Cairina* and *Anas*. In addition to this, the egg-cytoplasm coming from *Chrysolophus* must be largely permissible for the nuclear material coming from *Syrmaticus*, contrary to the relation existing in *Gallus* × *Phasianus*. Due to these two favourable situations, the germ-cells of this hybrid would advance up to the stage of the spermatid.

Here a consideration must be put on the effect of the egg-

cytoplasm for the foreign nuclear material in hybridization, where the nuclear material from the male parent enters the egg-cytoplasm from the female parent of different species. In this case it is highly probable that there exists a certain discordance between them. This discordance may be considered to be not so striking when the cells are in the undifferentiated state, such as the gonial or somatic cells. So that, in these cells the division of cells follows the normal course. But in the differentiated cells such as spermatocytes and spermatids, the discordance between the egg-cytoplasm and the nuclear material from the male parent becomes remarkable, effecting a disturbance to the development of the cell. This theory serves to illustrate the fact that the majority of germ-cells in the *Syrnaticus* \times *Chrysolophus* hybrid undergo degeneration in the stage of the spermatid.

It was pointed out in the foregoing section that a few cells metamorphosed into normal spermatozoa at least in appearance. Here we must consider the existence of the spermatid in which only the chromosomes originated from the female parent exist, though extremely small in proportion. The frequency (g) of occurrence of such a cell may be obtained by a formulae: $g = (1/2)^{n-1}$ where $n=41$. The spermatids would receive in such an extremely small proportion the complete set of the chromosomes of *Chrysolophus* (the female parent) in its own cytoplasm, namely of *Chrysolophus* and it is most probable that these spermatids may follow the regular course of spermioteleosis and develop into normal spermatozoa. By this consideration the formation of a few normal spermatozoa in the hybrid testis can be explicable. Very rare production of the offspring which is much alike the horse in the mating of the mule (♀) with the horse (♂), as reported by Anderson ('39), may be well understood also by this explanation. However from the fact that the number of seemingly normal spermatozoa in these hybrid testes is comparatively large, it seems to the author that—in order to make regular spermatogenesis possible, all the chromosomes in the spermatid need not to come from the female parent, but only certain chromosomes concerning the problem need.

Here some mentions should be given on the feature of the abnormal spermatozoa found in the hybrid testis. The nucleic part of these abnormal spermatozoa is generally separated into two distinct parts, the rod-shaped part of varying form and the spherical

part. These two parts are, as it seems to the author, may be different in origin; the rod-shaped part comes from *Chrysolophus* and the spherical part from *Syrmaticus*. It is probable that the chromatin came from *Chrysolophus* must be placed under a favourable condition in the spermatid, since it lies in its own cytoplasm, and therefore it may develop in some extent to form sperm-head, assuming rod-shape. The chromatin coming from *Syrmaticus* lies in the cytoplasm which came from *Chrysolophus*, and therefore it is destined to degenerate on account of unfavourable circumstance, showing pycnotic spherical form. In this way, the formation of abnormal spermatozoa in the hybrid testis can be explained.

It is quite natural to consider that the degeneration of the germ-cells in the female hybrid takes place by the same cause as occurred in the testis. The explanation for the phenomenon found in the male sex, therefore, must be applicable without change for the interpretation of the case of the female. The reason why the majority of germ-cells of the male develop up to the stage of spermatid, while all of the female degenerate in the stage of oocyte is attributed to the following fact: namely in the female a great deal of the vital energy may be consumed for the growth of ova and this accelerates the degeneration of the ova. Furthermore, if a few ova containing a good deal of the maternal chromosomes would be produced, they can not be ovulated, because the early degeneration of the greater parts of the female germ-cells will come to the degeneration of the ovary itself, and, on the one hand, if a few ova would have been grown large enough, they can not be layed, since the oviduct of such a hybrid does not develop beyond the embryonic state owing to the rudimentary ovary. Thus the female of this hybrid may be, different from the case of male, total sterile, though the fertility would be theoretically considered from the cytological point of view. This evidence was also made clear by the histological observations of the genital systems of the female hybrids in one and two years old.

Part III. Accounts regarding the hybrids between the Golden Pheasant, *Chrysolophus pictus* and the Lady Amherst Pheasant, *Chrysolophus amherstiae*

The Golden Pheasant, *Chrysolophus pictus* and the Lady Amherst Pheasant, *Chrysolophus amherstiae* are beautiful pheasants

commonly reared by bird-lovers, and it has long been known that the hybrids between these two species yield the offsprings for generations which are complete fertile. Due to scarcity of the nest bird, the Lady Amherst Pheasant has often been crossed with the Golden Pheasant, and the majorities of the birds we find in the cage of bird-dealers or aviculturists are thus hybrids between them. And it may be possible, by repeated back-cross, to make the hybrid birds closer to the either parental species in varying degrees desired.

As stated above this hybrid bird is quite easily obtainable, but no one has hitherto attempted the cytological observations either on the parents or on their hybrids. The fragmentary accounts on the plumage of this hybrid bird has already been published, but on genetical studies on the transmission of the colour of plumage have ever been tried, except that of Danforth & Sandnes ('39), who reported that the black mutant gene behaves as dominant in the hybrid of (*C. pictus* × *C. amherstiae*) × (*Ph. c. tenebrosus* × *Ph. c. mongolicus*).

The purpose of the present study is to make a close examination on the morphology of chromosomes and their behaviour in the germ-cells of this fertile interspecific hybrid by way of comparison with those of the sterile hybrids of some other crosses.

(1) *Anatomical and histological observations on the reproductive organs in the hybrid birds*

The hybrid bird herein studied possessed a pair of testes and the vas deferens normally developed in the regular position. The testes, measuring about 13 by 5 mm. long, are a little smaller than those of the normal male in the breeding season, due probably to the fact that the bird from which the testes were taken was 8 or 9 years old. By microscopical observations of the testis, it has been found that the seminal tubules are very well developed and the spermatogonial cells are also developed along the wall of the tubules forming several layers, inside which there are many primary and secondary spermatocytes in the process of active division or in the growing stage, showing quite regular arrangement of cells. Numerous spermatids in various stages of metamorphosis and well developed spermatozoa were also found occupying the central lumen of the tubule as shown in Pl. XXXVI, fig. 68. No signs of histological

abnormality or degeneration of cells were observed in the sections. Observations show that no conditions differ from those of the normal testis of pure line, and that spermatogenesis proceeds very regularly in this hybrid. Thus so far as the present study goes no structural modification was found in the testis of hybrid different from that of the pure bird. The spermatozoa are normally developed showing no deformity, and though the author could not make actual observations of the female gonad of this hybrid, there is no doubt that the female bird also possesses structurally normal reproductive organs, because of the well-known fact that the female birds regularly lay completely fertile eggs. These facts are sufficient to indicate that the hybrid birds normally propagate in their life. The cytological investigations given in the next part will make this evidence more valid.

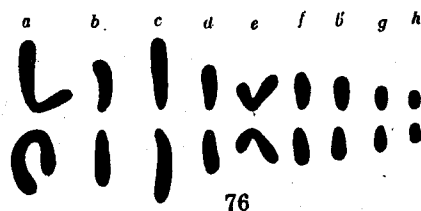
(2) *Chromosome studies on the parental species and their hybrids*

Detailed accounts on the chromosomes of the male parent of this hybrid, the Golden Pheasant, were given in the previous part. In this section the chromosomes of the Lady Amherst Pheasant and also those of the hybrid bird will be dealt with.

(a) *Chromosomes of the Lady Amherst Pheasant, Chrysolophus amherstiae*

Spermatogonial chromosomes. The spermatogonial chromosomes were studied at metaphase of the spermatogonial division found in the testes of an adult. The general morphological feature of chromosomes is quite similar to that observed in the Golden Pheasant, the total number of the chromosomes being 82. The garniture belongs to the typical avian type; the chromosomes are grouped into two clear size groups, the macro-chromosomes and micro-chromosomes. The macro-chromosomes consist of 18 (in 9 pairs) elements of which the first and the fifth pairs are represented by the V-shaped elements, as seen in the serial alignments (Textfig. 76). Especially noticeable, however, is the fact that the *b*-chromosome of this species seems to be represented by rather a short one, having the length of 0.71, while in the *c*-chromosome it is 1 unit

long, when the comparative relationship was estimated among the related forms such as the Common Pheasant and the Japanese Copper Pheasant. In the Golden Pheasant, as mentioned in the foregoing part, the *b*-chromosome seems also of the same condition.



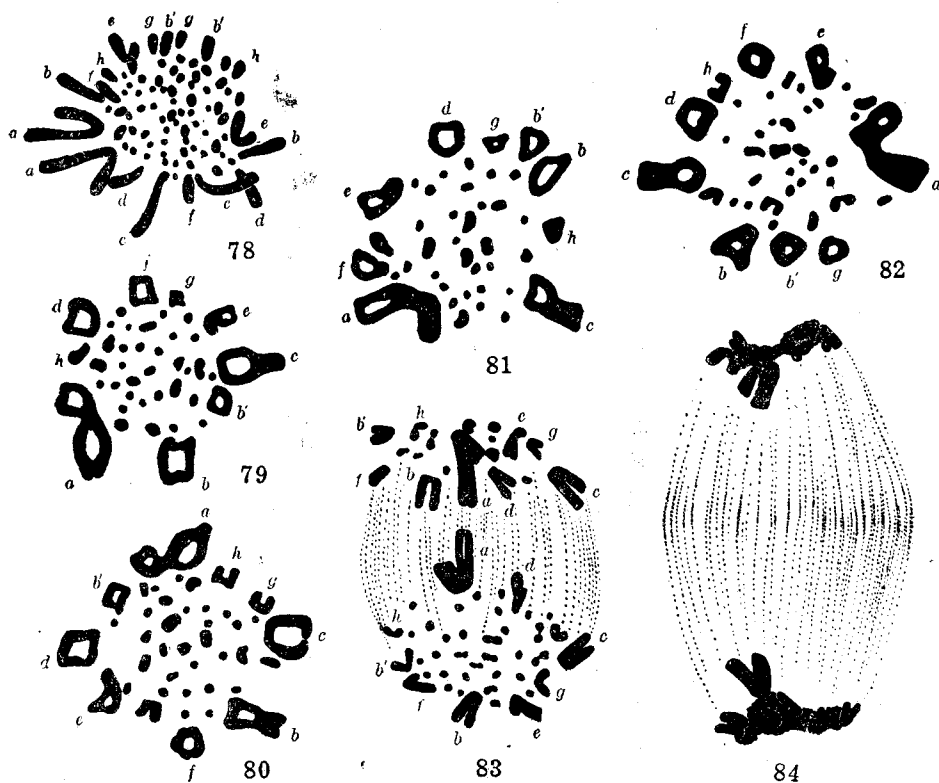
Textfigs. 76-77. Chromosomes of *Chrysolophus amherstiae*. $\times 4000$. 76. Serial alignment of macro-chromosomes from a spermatogonial metaphase. 77. Primary spermatocyte metaphase.

Spermatocyte chromosomes. A number of well preserved metaphase plates in the primary spermatocyte division were observed in the testis of an adult, examples of which are given in Textfig. 77. The morphological configuration of the chromosomes of spermatocytes is also not different from that of the Golden Pheasant. The haploid number 41 was thus determined without any conflict.

- (b) Chromosomes of the hybrid between the Golden Pheasant, *Chrysolophus pictus* and the Lady Amherst Pheasant, *Chrysolophus amherstiae*

Spermatogonial chromosomes. Textfig. 78 is a metaphase figure of spermatogonial division found in the testis of an adult hybrid bird. So far as the general appearance is concerned, the chromosomes of the hybrid are hardly distinguishable from those of the

parental species in its metaphase constitution. By careful observations the number of chromosomes is confirmed to be 82, the same as that of parental forms. The macro-chromosomes consist of also 18 elements of which the largest and fifth largest ones assume V-



Textfigs. 78-84. Chromosomes of the hybrid, *Chrysolophus pictus* × *Chrysolophus amherstiae*. ×4000. 78. Spermatogonial metaphase. 79-82. Primary spermatocyte metaphases. 83. Anaphase of the first division. In one of the daughter sets is found the complete haploid number of chromosomes, showing 41 elements. The segregation of bivalents thus takes place quite regularly. 84. Telophase of the same.

shape. The length of *b*-chromosomes is comparatively short as in the parental species, and their relative length calculated in the same way as that of the parents was nearly 0.7.

From the above observations it is evident that there are visible in the hybrid complement no morphological differences between the

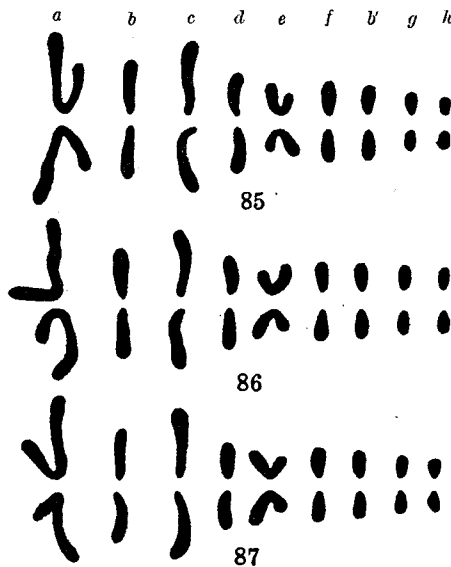
mates forming the homologous pair one of which is considered to be the chromosome derived from the parental form. Thus the evidence obtained indicates that the chromosomes of the hybrid form are impossible to be distinguished in every morphological respects from those of the parental species. The fact will be clear by reference to the accompanying figures showing the serial alignment of the chromosomes made by way of comparison between the hybrid and their parents (Textfigs. 85-87).

Spermatocyte chromosomes. The metaphase complexes of the primary spermatocytes are given in Textfigs. 79-82, which were observed in the testis of an adult. The number of chromosomes was determined to be 41, forming the haploid complex. Nine macro-chromosomes occupy the peripheral zone of the equatorial plates, surrounding the micro-chromosomes scattered in the central region. All the haploid elements observed in the primary spermatocyte are found having regular bivalent structure and the formation of univalent or multivalent chromosomes are not observable. In every respect of general morphological characters the chromosomes of the hybrid, therefore, do not differ from those of the parental species. Thus the meiotic divisions of this hybrid are sure to proceed in quite a normal manner, suggesting the production of functional gametes having regular chromosomal components.

(c) Morphological analysis of the hybrid chromosomes

From the observations stated above the following statement can be made that, so far as the morphological characteristics are concerned, no significant difference is found in the chromosome complex between the Golden Pheasant and the Lady Amherst Pheasant, as well as in those among the latter and the hybrid between them. This fact is emphasized by comparing the Textfigs. 55-58 and 76 with Textfigs. 85-87, in which we find, at least from the morphological view point, they are nearly identical with one another. It is remarkable and noteworthy that there occurs no asymmetrical element in the chromosome garniture of this hybrid form, which is usually found in the chromosome sets of the following hybrids as *Cairina* \times *Anas*, *Gallus* \times *Phasianus*, and even *Syrnaticus* \times *Chrysolophus* as noted in the previous parts. As mentioned in the foregoing descriptions, the chromosomal elements of this hybrid form

are all sorted into homologous mates of identical shape and size two by two, and they constitute regular bivalent chromosomes by pairing in the primary spermatocyte division, showing the haploid number of 41 which is a complete half set of the diploid garniture.



Textfigs. 85-87. Serial alignments of spermatogonial macro-chromosomes of the hybrid, *Chrysolophus pictus* × *Chrysolophus amherstiae*. ×4000.

These observations are sufficient to show that there is a complete identity between the parental chromosomes and those of the hybrid form, not only in their external features but also in their inner structure.

(3) Behaviour of germ-cells in the F_1 hybrid

The multiplying divisions of the spermatogonial cell of this hybrid proceed in a quite regular manner as shown in the foregoing observations. The cells then enter into the course of the growing period of the auxocyte. In Pl. XXXVI, fig. 69 are shown the spermatocytes in various stages such as leptotene, bouquet, pachytene, etc. These cells show no trace of abnormality in these stages. Passing through diakinesis stage, the spermatocytes complete

normally the growth and the conjugation of chromosomes, and enter metaphase of the first division. The metaphase chromosomes are quite regular in their form, structure, arrangement and behaviour, and there is nothing different from those found in pure species in every respect (Pl. XXXVI, fig. 70). Thus, the segregation of chromosomes during meiosis takes place quite regularly in the testis of this hybrid, as occurs in pure line (Textfigs. 83-84). The primary spermatocytes thus produce two functional secondary spermatocytes, and then they are divided into four cells, the spermatids. The course of metamorphosis of spermatids into spermatozoa proceeds also very regularly, thus many functional spermatozoa are produced (Pl. XXXVI, fig. 71). The regular behaviour of spermatids during spermioteleosis will be more clearly understood by comparing these figures with Pl. XXXVI, figs. 72, 73 in which is shown the general course of spermatogenesis of the Korean Ring-necked Pheasant, *Phasianus colchicus karpowi*. As above noted, all circumstances encountered in the testis of this hybrid show no slightest evidence of abnormality, and no difference is found from those occurred in the bird of pure line.

(4) Discussion

Different types of the bird hybrids that are fertile have been reported by the present author. One of these types is found in the male of the hybrid, *Syrnaticus soemmerringii* \times *Chrysolophus pictus* (see Part II). In the male belonging to this type some amount of the normal spermatozoa seemed to be yielded, and consequently this hybrid male must be of very low infertility. It is possible to say that a small number of cells must be developed into the functional spermatozoa passing through the normal course of spermatogenesis and the majority of germ-cells must be degenerated. The second type is seen in the male of the hybrid pigeon, *Streptopelia orientalis* \times *Streptopelia decaocto* (Yamashina '41a). In this type the functional spermatozoa are yielded very abundantly, but a few of germ-cells go into degeneration. Therefore the bird seemed to show rather high fertility than in the former case. In the third type represented by the hybrid, *Chrysolophus pictus* \times *Chrysolophus amherstiae* which is now concerned, very high fertility has been proved as in the second type. All the germ-cells in the testis of

the latter hybrid differentiate into functional spermatozoa through the normal course of spermatogenesis, and none of cells degenerate. Each of these three types is found to be fertile in nature, but the difference existing among them is found in the following point: in the first and second types only a part of the germ-cells develops into functional spermatozoa and the rest of them degenerate, but in the third type all the germ-cells develop into spermatozoa with normal function throughout the regular course of spermatogenesis without showing any degeneration of cells in the testis.

The occurrence and arrangement of germ-cells within the seminal tubules of the hybrid are entirely normal in the third type. The germ-cells are arranged in the seminal tubule in the order of spermatogonia, primary spermatocytes, secondary spermatocytes, spermatids in process of metamorphosis and mature spermatozoa, the latter being collected in the lumen of the tubule in definite groups (Pl. XXXVI, fig. 68). The conditions thus show nothing irregular and different from those found in the testis of pure bird (Pl. XXXVII, figs. 74, 75). But in the seminal tubules of the first and second types the arrangement of germ-cells shows to be irregular in some degree, due probably to the degeneration of some of the germ-cells (Pl. XXXII, figs. 47, 48). In every respect, the bird of the third type of the hybrid as above mentioned does not differ from the pure normal bird and can be called as having perfect fertility, and, therefore, the first and second types may be of imperfect fertile or weak sterile comparing to the complete sterile hybrids having no reproductive function, such as the hybrid, *Cairina* × *Anas* and *Gallus* × *Phasianus*.

To consider the cause of complete fertility of the hybrids as found in the third type the following two factors come under consideration: The one is the complete similarity of the parental chromosomes, and the other also the complete identity of the cytoplasmic conditions in parental forms.

The present observations made upon the germ-cells of the third type hybrid show that the perfect conjugation between each homologous chromosome occurs in meiosis, and the behaviour of chromosomes is quite normal in the later course of spermatogenesis. This evidence is sufficient to suggest the fact that the chromosomes of the *Chrysolophus pictus* are entirely similar to those of the

Chrysolophus amherstiae not only in their external morphology but also in their inner structural condition. If the chromosomes are dissimilar, the behaviour of chromosomes becomes irregular in some degree in the course of meiotic process, the examples of which are known in the hybrids *Syrnaticus* × *Chrysolophus*, *Cairina* × *Anas* and in the case of the hybrid, *Gallus* × *Phasianus*.

Many examples showing that hybrids between the parents having a similar chromosome complex are of a complete fertility, have already been known in the interracial crosses of domestic animals, such as the Domestic fowl (Pl. XXXVII, figs. 76-79) and the gold fish (Makino '41). The racial hybrids of the domestic dove may perhaps be the case. Smith ('12) once reported that the racial hybrids between the Magpie dove and the Common dove are sterile by the occurrence of abnormal spermatogenesis, but the reinvestigation attempted by Prof. Oguma with the same cross revealed that this interracial hybrid also possess normal fertility (Oguma, unpublished; cf. Yamashina '41, p. 11).

The same condition is also found in the subspecies hybrids of some wild animals. According to Dice ('33) all hybrids he observed between the subspecies of mice belonging to the genus *Peromyscus* were completely fertile. Also, the hybrid between the Japanese Green Pheasant, *Phasianus colchicus versicolor* and the Korean Ring-necked Pheasant, *Phasianus colchicus karpowi* has well been known to produce fertile offsprings. The chromosome complements of these birds are entirely identical not only in morphology but in other structural characteristics, as clearly demonstrated in this investigation. The fertility of the similar species cross was proved by Makino ('41a) who had succeeded crossing between the domesticated mouse, *Mus musculus* L. and the wild mouse, *Mus molossinus* Temm. & Schl. There is no doubt that the hybrid between *Chrysolophus pictus* and *Chrysolophus amherstiae* must be involved in this category.

Here the conclusive statement is to be emphasized that for the perfect fertility in the hybrid the identity of both the genome and cytoplasm is required between the parental forms. The interrelation between the chromosomes and cytoplasm is very important and can not be neglected in the consideration of hybrid sterility, especially in the case of animal.

Conclusion

Based on the results obtained in this study and from those in the former studies (Yamashina '40, '41a, '41b) which were exclusively undertaken on sterility in hybrid birds, the possible conclusion may be presented as below.

Though certain peculiar genes which make the offsprings sterile have been known to occur in the hybrids of certain insects—the genic sterility—(Goldschmidt '32, '34, Pariser '27, Dobzhansky '34, '36, '37, Lancefield '29), all the cases of sterility so far observed in hybrid birds are, it seems to the author, sterility of the chromosomal type. Thus, sterility occurring in hybrid birds is considered not attributable to special gene or genes but to depend primarily upon the chromosomal dissimilarity.

If the difference between the chromosomes of the parental forms is large enough, the degeneration of the germ-cell would commence early in the beginning of the growing period of the auxocyte such as the leptotene and pachytene stage. The example of this case was shown in the hybrid, *Gallus* × *Phasianus*, which was fully discussed in the Part I. If this chromosomal dissimilarity is not so large between the parental forms as in the latter case, the gametogenesis would advance to the first maturation division. The hybrid between *Cairina* and *Anas* reported in the author's previous paper (Yamashina '41b) belongs to this type of sterility. The hybrid obtained from the cross between *Syrnaticus* and *Chrysolophus*, in which gametogenesis is sometimes normally carried on, but in the most cases it is disturbed during spermioteleosis, is considered to depend on very slight dissimilarity of the chromosomes between the two parents.

The above explanation of the chromosomal dissimilarity may be more easily understood by assuming a compensatory factor in the hybrid sterility. It is the antagonistic relation existing between the nuclear material coming from the one parent and the cytoplasm originated from the other parent. If the relation between the paternal chromosomes and maternal cytoplasm is very harmonious owing to close similarity in their nature, the germ-cells would survive for very long duration, and the process of degeneration of germ-cells resulting from the chromosomal dissimilarity may be compensated to some extent. But in the reversed condition, the degeneration of

germ-cells would be accelerated. The disturbance of spermioteleosis found in the hybrid *Syrmaticus* × *Chrysolophus* seems to be resulted in the role of this factor as already discussed.

Therefore, the cause of sterility found in the hybrid birds may be responsible to two factors; the one is the dissimilarity of the chromosomes between the parental forms, and the other the disharmonious relation existing between the maternal cytoplasm and paternal chromosomes. Depending on the degree of combination of these two factors, the degeneration of germ-cells may take place in early stage of gametogenesis, as occurred in the *Gallus* × *Phasianus* hybrid, or sometimes in later stage as in the case of *Syrmaticus* × *Chrysolophus*. The hybrid between the Golden Pheasant, *Chrysolophus pictus* and the Lady Amherst Pheasant, *Chrysolophus amherstiae*, in which gametogenesis is carrying on quite regularly, is an instance in which the chromosomes are entirely identical in structure between both parents, and at the same time the cytoplasmic relation is also quite harmonious between them as in the case of the racial cross. In the light of these two factors, the possible interpretation for sterility in the hybrid cross will be made quite clear.

Summary

The present paper deals with the cytological investigations of the hybrid, *Gallus gallus* × *Phasianus colchicus*, *Syrmaticus soemmerringii* × *Chrysolophus pictus* and *Chrysolophus pictus* × *Chrysolophus amherstiae*. The results obtained are to be summarized as below.

1. The chromosomes of the Domestic fowl, *Gallus gallus* var. *domesticus* were thoroughly investigated on the several races (the Shamo, the Shamo Bantam, the Chabo, the Ukokkei, the White Leghorn, the Nagoya, etc.), and their number and other morphological characteristics such as the shape and size were made clear. The diploid number of the male was decided to be 78 (σ , $2n$) and that of the female was 77 (φ , $2n$) in each race observed.

2. The chromosomes of the Common Pheasant, *Phasianus colchicus* was investigated in the two subspecies (*Ph. colchicus karpowi* and *Ph. colchicus versicolor*) with the purpose of determining the number and other morphological features. The diploid numbers were determined to be 82 (σ , $2n$) in the male, and 81

(♀, $2n$) in the female, in each subspecies studied. The haploid number observed in the primary spermatocyte was 41 (♂, n) without exception.

3. Many F_1 hybrids were produced between the Domestic fowl and the Common Pheasant from various combinations of the parents. The karyological study of these hybrid birds shows that the chromosome complex of the hybrid consists of the total sum of the haploid chromosome complex of two parents. That is, diploid number obtained in the male hybrid was 80 (♂, $2n$), and that of the female hybrid 79 (♀, $2n$).

The male germ-cells of this hybrid do not advance beyond the pachytene stage of the primary spermatocyte, and thereafter they degenerate failing to form the metaphase spindle of the first division. It was found that the degeneration of the oocyte seems to take place during the leptotene stage. Thus, complete sterility of these hybrids was cytologically proved.

4. The chromosomes of the Japanese Copper Pheasant, *Syrnaticus soemmerringii scintillans* were studied in the male. The number of chromosomes was shown to be 82 in diploid (♂, $2n$) and 41 in haploid (♂, n), fully agreeing with those of the Common Pheasant. The morphological characteristics of the chromosomes of *Syrnaticus* assume also a close resemblance to those of *Phasianus*, excepting a fact that the length of the *b*-chromosomes of the former species is slightly longer than that of the latter.

5. It was found that the number of chromosomes of the Golden Pheasant, *Chrysolophus pictus* was 82 in diploid (♂, $2n$) and 41 in haploid (♂, n), showing a complete agreement with those found in the Common Pheasant and the Japanese Copper Pheasant. The morphological feature of the chromosomes was also found to be nearly same with each other, and only visible difference lies in the length of the *b*-chromosome which is clearly shorter in the Golden Pheasant than in the Common Pheasant.

6. The karyological investigation was made on the hybrid between the Japanese Copper Pheasant and the Golden Pheasant. The diploid number of the chromosomes was observed to be completely the same as the parental species, showing 82 chromosomes in the male (♂, $2n$).

In the testes of this hybrid bird the majority of the germ-cells form the metaphase spindle of the first meiotic division. The pairing

of chromosomes in meiosis was found to take place in the normal manner, the haploid number (41) being observed without difficulty. Some of these cells seem to degenerate and fail to complete the second meiotic division, resulting the formation of the binucleated spermatids; some of the others seems to pass through the second division. Of these cells a larger part is destined to form abnormal shaped spermatozoa, and a small part of them seems to develop into the spermatozoa of normal shape. Thus the partial fertility of this hybrid was suggested, as far as the male hybrids are concerned.

7. The karyotype of the Lady Amherst Pheasant, *Chrysolophus amherstiae* was found to be quite the same as that of the Golden Pheasant, *Chrysolophus pictus*, either in the number of chromosomes or in the other morphological characters.

The cytological investigation carried out on the testis of the hybrid, the Golden Pheasant \times the Lady Amherst Pheasant, shows there exist no slightest abnormality in the meiotic behaviour of germ-cells. The number of chromosomes was found quite the same as those existing in the parental forms, numbering 82 in diploid (δ , $2n$) and 41 (δ , n) in haploid. They pass through two meiotic divisions in normal way and finally develop into functional spermatozoa. So far as the male individuals of this hybrid are concerned, therefore, it is beyond doubt that they are completely fertile.

8. Sterility occurring in the hybrid, *Gallus* \times *Phasianus* and *Syrnaticus* \times *Chrysolophus*, as mentioned above, is undoubtedly of the chromosomal. Another compensatory factor leading to sterility is adopted for the interpretation of hybrid sterility. That is the antagonistic relationship existing between the nuclear element coming from the one parent (δ) and the cytoplasm originated in the other parent (φ). In case when the chromosomal dissimilarity is very large between the parental species and at the same time the paternal nuclear element is not harmonious with the maternal cytoplasm, the degeneration of the hybrid germ-cells occurs very early in meiosis, the instance of which is found in the hybrid, *Gallus* \times *Phasianus*. If the chromosomal dissimilarity is extremely small between the parents and further the nuclear cytoplasmic relation is quite harmonious; the degeneration of the hybrid germ-cells takes place in the later stage of meiosis, example being obtained in the hybrid, *Syrnaticus* \times *Chrysolophus*.

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Explanation of Plate XXIII

Four males of the hybrid between the Domestic fowl, *Gallus gallus* var. *domesticus* and the Common Pheasant, *Phasianus colchicus*.

- Fig. 1. Red-hackled Shamo ♂ × *Phasianus colchicus karpowi* ♀.
- Fig. 2. Black Shamo ♂ × *Phasianus colchicus karpowi* ♀.
- Fig. 3. *Phasianus colchicus versicolor* ♂ × Shamo ♀.
- Fig. 4. *Phasianus colchicus versicolor* ♂ × Chabo ♀.

Explanation of Plate XXIV

The hybrids between the Japanese Copper Pheasant, *Syrnaticus soemmerringii scintillans* ♂ and the Golden Pheasant, *Chrysolophus pictus* ♀, and their parent birds.

- Fig. 5. Male hybrid.
- Fig. 6. Female hybrid.
- Fig. 7. Male of *Syrnaticus soemmerringii scintillans*.
- Fig. 8. Male of *Chrysolophus pictus*.

Explanation of Plate XXV

- Fig. 9. Spermatogonial metaphase of the Shamo, *Gallus gallus* var. *domesticus*. ×2200.
- Fig. 10. Oogonial metaphase of the same. ×2200.
- Figs. 11–12. Spermatogonial metaphases of *Phasianus colchicus karpowi*. ×2200.
- Fig. 13. Primary spermatocyte metaphase of the same. ×2200.
- Fig. 14. Oogonial metaphase of the same. ×2200.

Explanation of Plate XXVI

All are from the hybrid, the Red-hackled Shamo, *Gallus gallus* var. *domesticus* ♂ × *Phasianus colchicus karpowi* ♀.

- Fig. 15. Longitudinal section of the embryonal testis. 11 days old embryo of the hybrid. ×100.
- Fig. 16. Enlarged view of the same testis, showing the regular feature of seminal tubules. ×400.
- Fig. 17. Ventral view of the reproductive system of the 6 months old male of the same hybrid. ca. ×1.
- Fig. 18. Section of a part of the testis of the 6 months old hybrid, showing the regular arrangement of the seminal tubules, which have, however thin, nearly the same diameter as that of the 30 days old chick. ×100.
- Fig. 19. Cross-section of the vas deferens of the 6 months old hybrid. ×100.

Explanation of Plate XXVII

All are from the hybrid, the Red-hackled Shamo, *Gallus gallus* var. domesticus ♂ × *Phasianus colchicus karpowi* ♀.

- Fig. 20. Section of a part of the testis of the 10 months old male hybrid. In the seminal tubules there are observable numerous primary spermatocytes in the early stage of the growing period. ×100.
- Fig. 21. Section of a part of the testis of the 22 months old male hybrid. In some seminal tubules are contained spermatocytes which have undergone degeneration. ×100.
- Fig. 22. Enlarged view of the same testis. The seminal tubules contain the spermatogonial cells in resting condition. ×400.
- Fig. 23. Cross section of the vas deferens of the same hybrid. ×100.
- Fig. 24. Section of the testis of the 24 months old male having been injected with Testosteron and Puberogen. The development of the interstitial tissues becomes active. ×100.

Explanation of Plate XXVIII

All are from the hybrid, the Red-hackled Shamo, *Gallus gallus* var. domesticus ♂ × *Phasianus colchicus karpowi* ♀.

- Fig. 25. Section of the ovary of 11 days old embryo. Many oogonia in the process of active division were found in the germinal epithelium of this ovary. ×100.
- Fig. 26. Section of the ovary of the female chick just hatched. None of the developed follicle is found among the tissues. ×100.
- Fig. 27. Enlarged view of the same ovary, showing the oocytes which do not advance beyond the leptotene stage. ×400.
- Fig. 28. Ventral view of the reproductive system of the 12 months old female (adult). ov: ovary. od: oviduct. ca. ×1.
- Fig. 29. Section of the ovary of the same specimen. ×30.

Explanation of Plate XXIX

- Fig. 30. Section of a part of the ovary of the hybrid, the Red-hackled Shamo, *Gallus gallus* var. domesticus ♂ × *Phasianus colchicus karpowi* ♀ (the same specimen of Pl. XXVIII, figs. 28, 29). Many degenerating oocytes are shown. ×400.
- Fig. 31. Section of the uterus portion of the oviduct of the same hybrid which is the embryonal state in condition. ×40.

- Fig. 32. Longitudinal section of the fallopian tube of the same female, which opens in its free end. $\times 40$.
- Fig. 33. Section of the testis of the 22 months old hybrid, *Phasianus colchicus versicolor* $\sigma \times$ the Shamo, *Gallus gallus* var. domesticus φ . $\times 100$.
- Fig. 34. Enlarged view of the above testis. Many primary spermatocytes in the early growing stages are found occupying the lumen of the tubules. $\times 400$.
- Fig. 35. Section of the testis of the 14 months old hybrid, *Phasianus colchicus* $\sigma \times$ the Chabo, *Gallus gallus* var. domesticus φ . The development of the seminal tubules is rudimentary, none of the spermatocyte in the growing period being found in the tubules. The interstitial cells were found developed among seminal tubules. $\times 100$.
- Fig. 36. Section of the testis of the 22 months old hybrid, the Red-hackled Shamo, *Gallus gallus* var. domesticus $\sigma \times$ *Phasianus colchicus karpowi* φ (the different specimen from that of Fig. 21). $\times 100$.

Explanation of Plate XXX

All are from the hybrid, the Red-hackled Shamo, *Gallus gallus* var. domesticus $\sigma \times$ *Phasianus colchicus karpowi* φ .

- Fig. 37. Section of a part of the embryonal testis, showing regular multiplying mitotic division of the spermatogonial cells. From the 13 days old embryo. $\times 400$.
- Fig. 38. Enlarged view of the same, showing the spermatogonia in metaphase and anaphase. $\times 1000$.
- Fig. 39. Section of a part of the testis of the 22 months old hybrid, the Red-hackled Shamo, *Gallus gallus* var. domesticus $\sigma \times$ *Phasianus colchicus karpowi* φ , showing some of the spermatogonia being in process of division. $\times 600$.
- Fig. 40. The same as above. $\times 600$.
- Fig. 41. Section of the testis of the same hybrid, showing a seminal tubule, which contains some primary spermatocytes in the leptotene stage. $\times 600$.

Explanation of Plate XXXI

All are from the hybrid, the Red-hackled Shamo, *Gallus gallus* var. domesticus $\sigma \times$ *Phasianus colchicus karpowi* φ .

- Fig. 42. Section of the testis of the 22 months old hybrid (the same specimen of Pl. XXX), showing a seminal tubule which contains many primary spermatocytes in leptotene and bouquet stage. $\times 600$.

- Fig. 43. The same, showing primary spermatocytes in the pachytene stage. $\times 600$.
- Fig. 44. The same, showing primary spermatocytes which take the course of degeneration from the pachytene stage. Note the pycnotic cells contained in the lumen of the tubule. $\times 600$.
- Fig. 45. The same, showing spermatocytes in the course of degeneration in the lumen of the tubules. $\times 600$.
- Fig. 46. The same, showing some degenerating spermatocytes in the lumen. $\times 600$.

Explanation of Plate XXXII

All are from the hybrid, *Syrmaticus soemmerringii scintillans* ♂ \times *Chrysolophus pictus* ♀.

- Fig. 47. Section of the testis of the adult male, showing several seminal tubules containing a large number of germ-cells which are somewhat irregular in arrangement. $\times 100$.
- Fig. 48. Section of a part of the seminal tubules, in which meiotic processes of germ-cells actively advance. $\times 400$.
- Fig. 49. The same. Numerous degenerating germ-cells and abnormal spermatozoa are found in the lumen of the tubules. $\times 400$.
- Fig. 50. Ventral view of the reproductive system of the adult female (10 months old). The surface of the ovary (indicated with *ov.*) is smooth, but seven follicles of about 2 mm. in diameter are attached here and there on it. The oviduct (indicated with *od.*) is very rudimentary in appearance. ca. $\times 1$.
- Fig. 51. Section of a part of the ovary of the above specimen. None of the oocytes is seen, germinal epithelium having been filled with highly developed connective tissues. $\times 100$.

Explanation of Plate XXXIII

All are from the adult female hybrid, *Syrmaticus soemmerringii scintillans* ♂ \times *Chrysolophus pictus* ♀.

- Fig. 52. Section of a part of the uterus portion of the oviduct, showing a quite rudimentary development. From the 10 months old female (the same as Pl. XXXII, figs. 50, 51). $\times 100$.
- Fig. 53. Longitudinal section of the fallopian tube of the same specimen, to show the opening of its free end. $\times 100$.

- Fig. 54. Ventral view of the reproductive system of the 22 months old female. Superficially the ovary and the oviduct as well, have more advanced rudimentary structure than those of the 10 months old female. *ov*: ovary. *od*: oviduct. *ca*. $\times 1$.
- Fig. 55. Section of a part of the ovary of the above specimen. Many abortive follicles are seen. $\times 100$.
- Fig. 56. Section of the uterus portion of the oviduct of the above specimen, showing the rudimentary condition of the tissue. $\times 100$.

Explanation of Plate XXXIV

All are from the adult hybrid, *Syrnaticus soemmerringii scintillans* ♂ \times *Chrysolophus pictus* ♀.

- Fig. 57. Section of the testis, showing multiplying divisions of the spermatogonia. The division is quite normal. $\times 1200$.
- Fig. 58. The same, showing the primary spermatocytes in the growing period. $\times 400$.
- Figs. 59-60. The primary spermatocyte metaphase plates found in the same testis. 41 bivalents are contained in each plate. $\times 2200$.
- Fig. 61. A part of the seminal tubule of the same specimen, showing many degenerating spermatids. $\times 1200$.

Explanation of Plate XXXV

All are from the adult male hybrid, *Syrnaticus soemmerringii scintillans* ♂ \times *Chrysolophus pictus* ♀.

- Fig. 62. Beginning of degeneration of the binucleated spermatid. $\times 900$.
- Fig. 63. Binucleated spermatid in pycnotic degeneration. $\times 900$.
- Fig. 64. The same. In one of the two nuclei begins to develop a rod-like body. $\times 900$.
- Fig. 65. A part of the seminal tubule, showing many spermatids in the early stage of spermioteleosis. $\times 1200$.
- Fig. 66. The same, showing many spermatids in later stages of abnormal spermioteleosis. $\times 1200$.
- Fig. 67. The same. $\times 1200$.

Explanation of Plate XXXVI

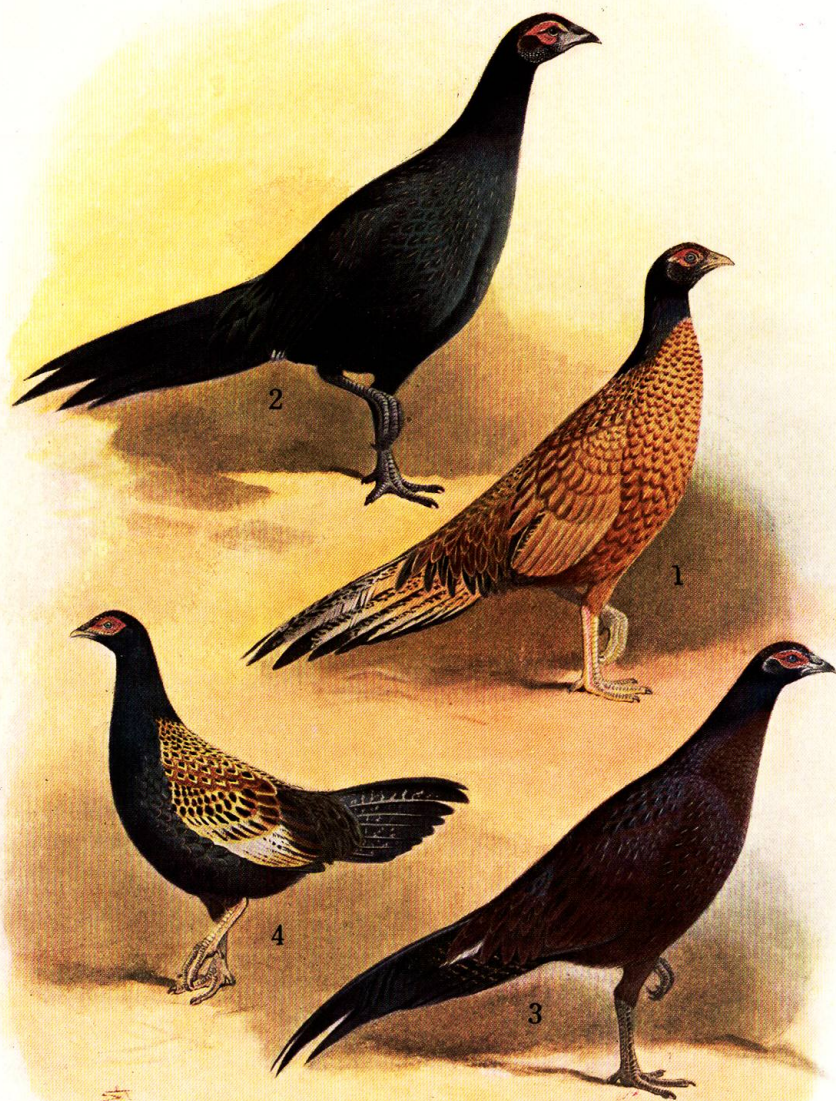
Figs. 68-71 are from the adult male hybrid, *Chrysolophus pictus* ♂ \times *Chrysolophus amherstiae* ♀, and Figs. 72-73 from *Phasianus colchicus karpowi*.

- Fig. 68. Section of a part of the testis, showing the regular arrangement of the germ-cells in the seminal tubules. $\times 100$.

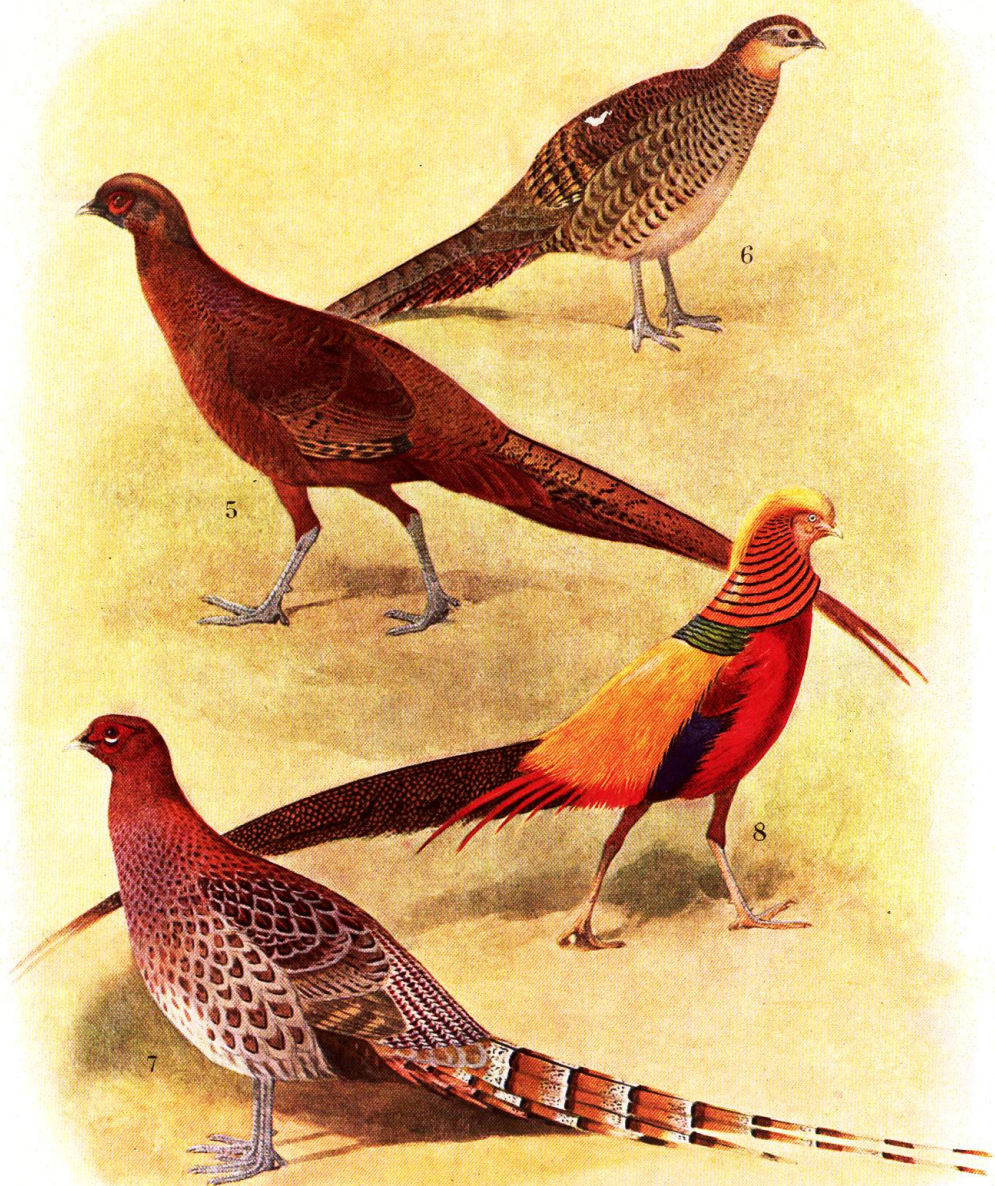
- Fig. 69. Section of a part of the seminal tubule of the above testis. Numerous primary spermatocytes are in the growing period. $\times 600$.
- Fig. 70. The same, showing many primary spermatocytes in metaphase. $\times 400$.
- Fig. 71. The same, showing various stages of spermioteleosis. $\times 600$.
- Figs. 72-73. A part of the seminal tubule of the Korean Ring-necked Pheasant, *Phasianus colchicus karpowi*, showing various stages of spermioteleosis. $\times 600$.

Explanation of Plate XXXVII

- Figs. 74-75. A part of the seminal tubule of the Korean Ring-necked Pheasant, *Phasianus colchicus karpowi*. Various stages of spermioteleosis are shown. 74: $\times 600$. 75: $\times 400$.
- Figs. 76-79. From the interracial hybrid of the Domestic fowl (White Leghorn $\sigma \times$ Shamo φ).
- Fig. 76. Section of the seminal tubule, showing active spermatogenesis. $\times 400$.
- Fig. 77. The same, showing many primary spermatocytes in the growing period. $\times 600$.
- Fig. 78. The same, showing many primary spermatocytes in the metaphase and numerous spermatids. $\times 600$.
- Fig. 79. The same, showing active spermioteleosis. $\times 600$.
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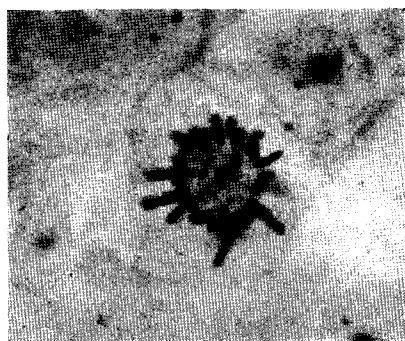
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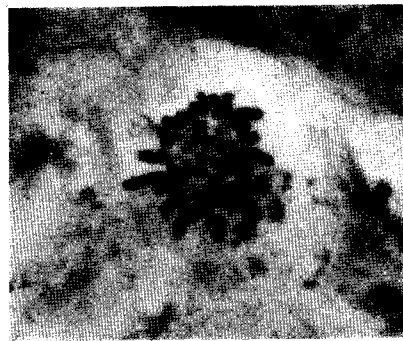
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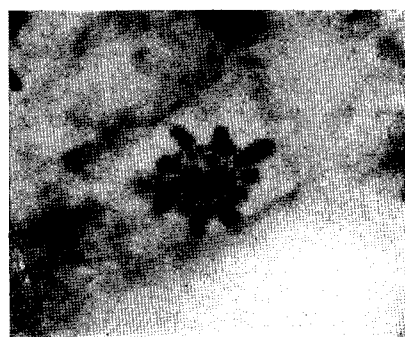
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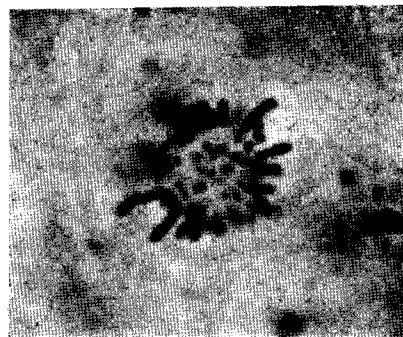
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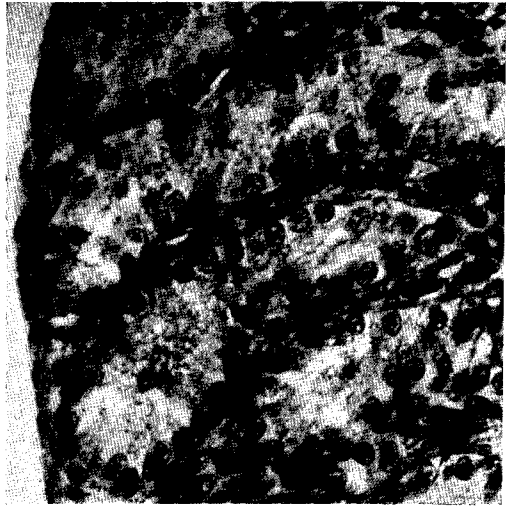
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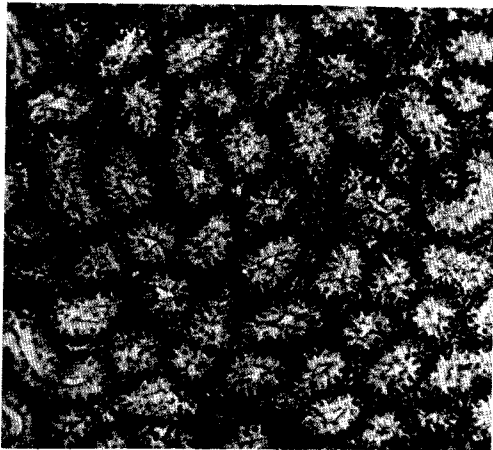
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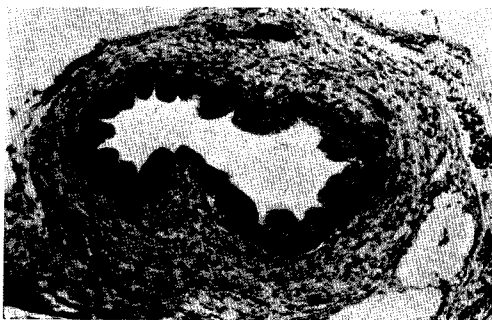
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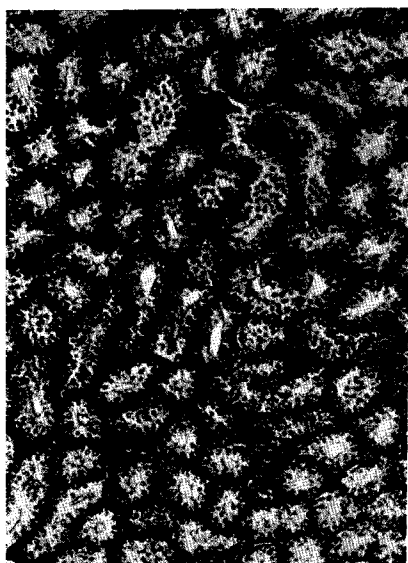
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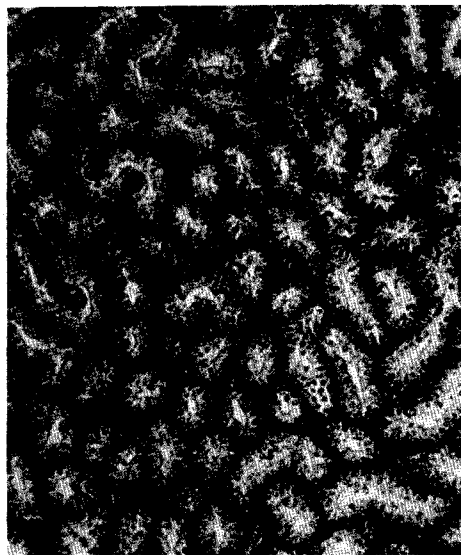
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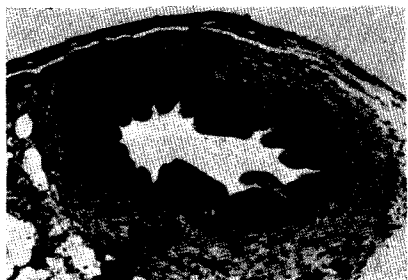
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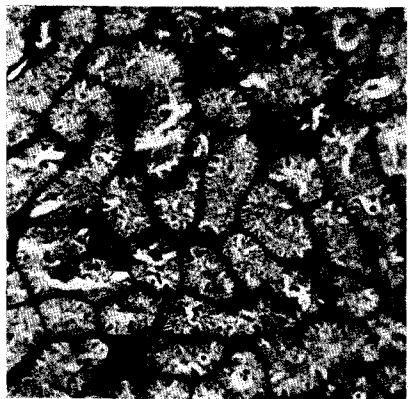
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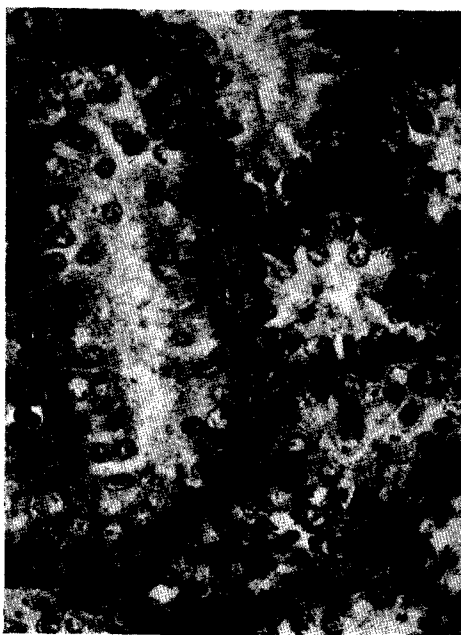
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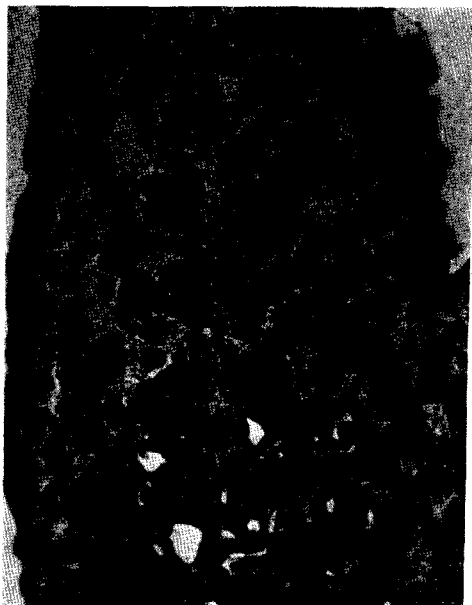
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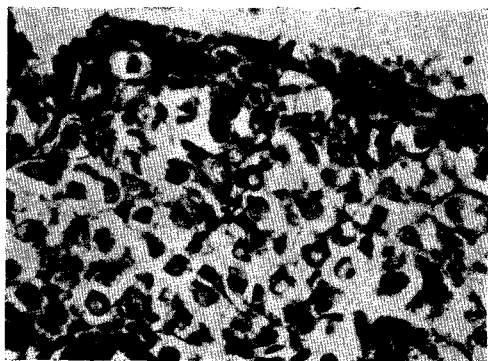
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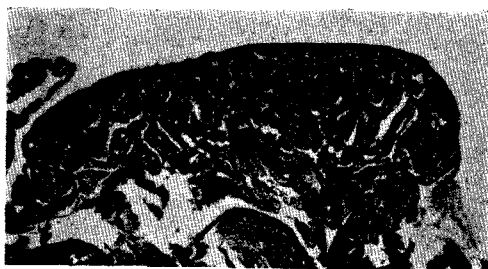
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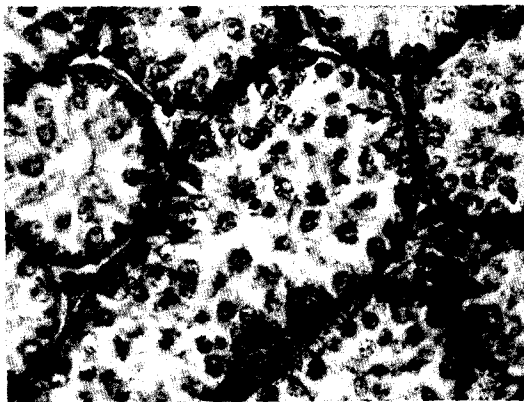
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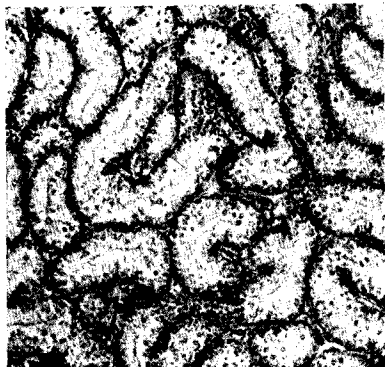
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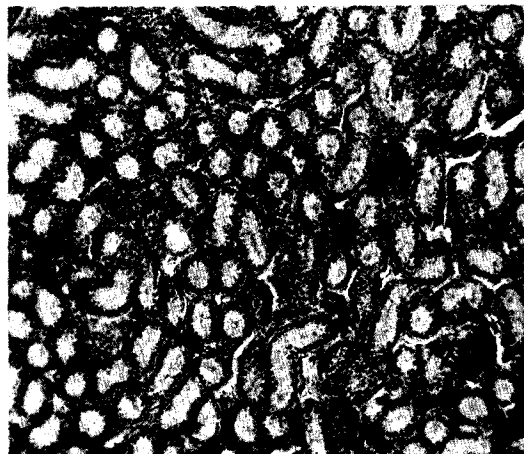
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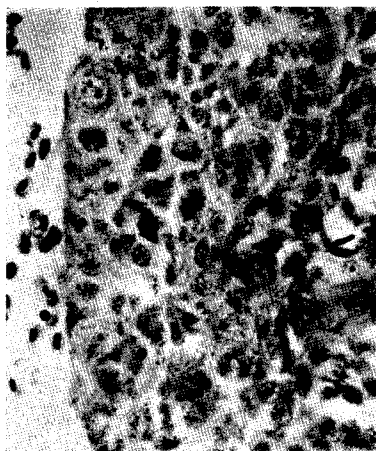
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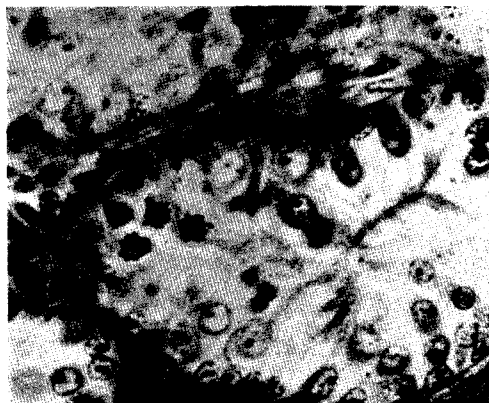
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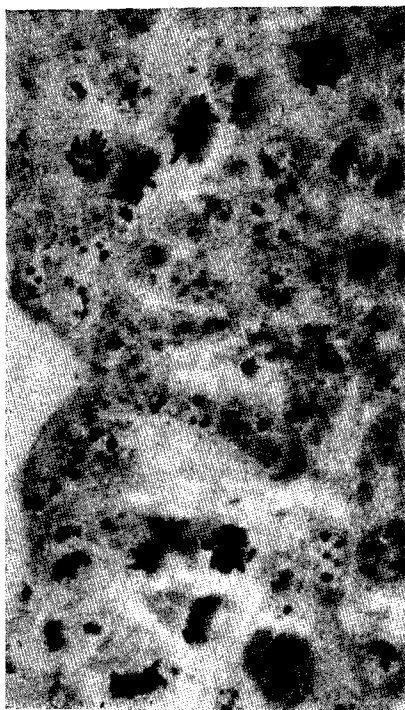
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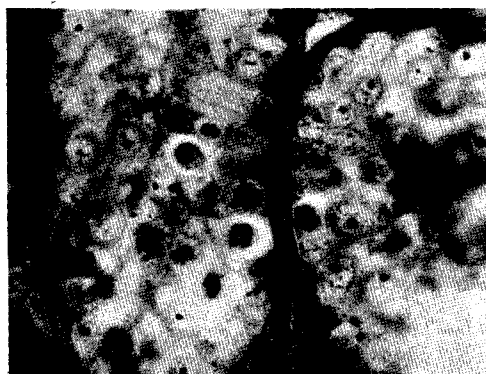
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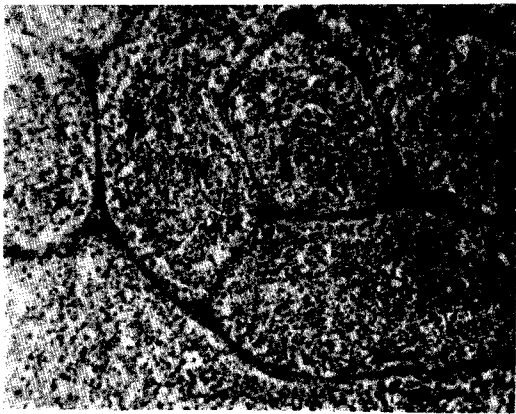
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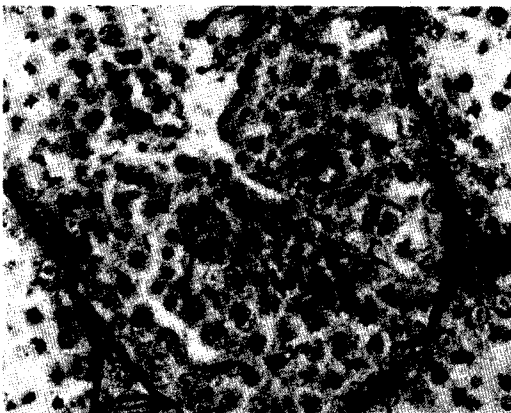
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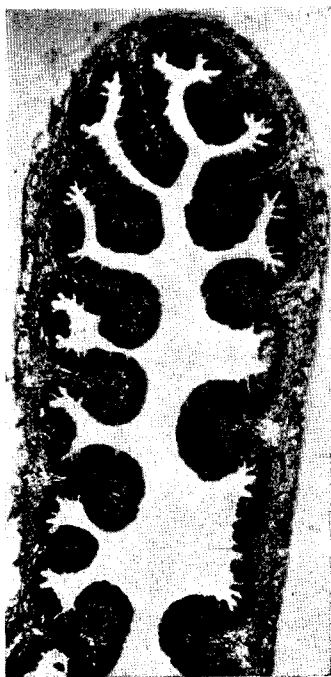
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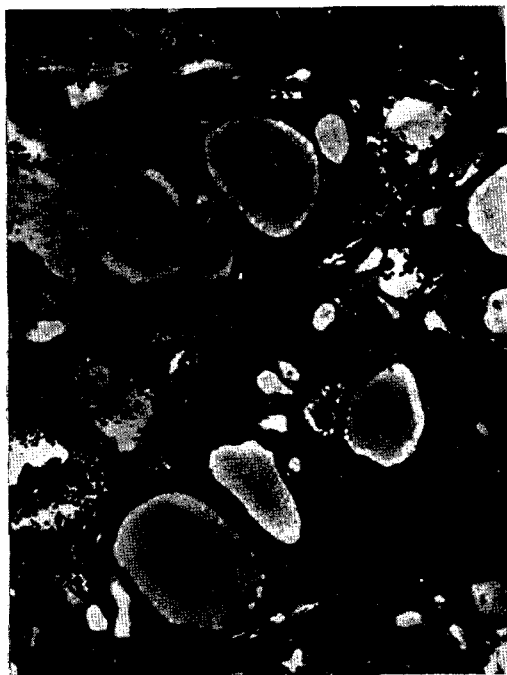
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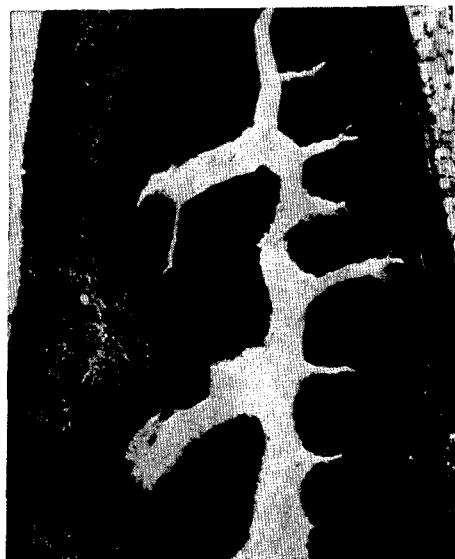
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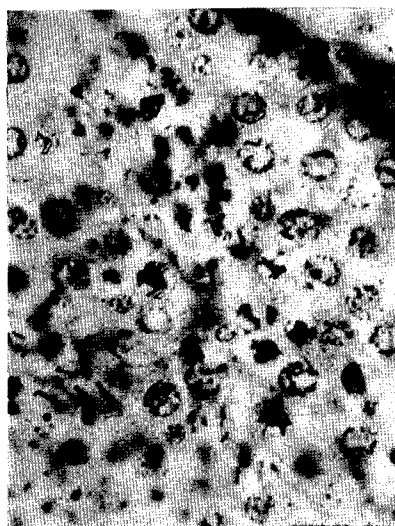
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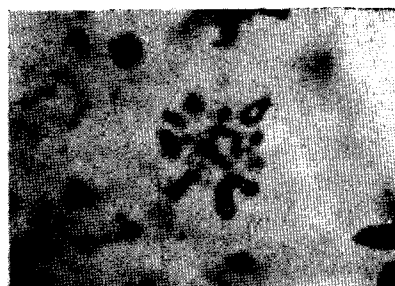
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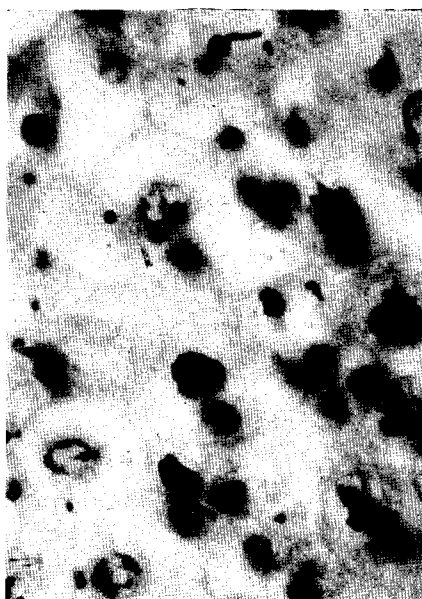
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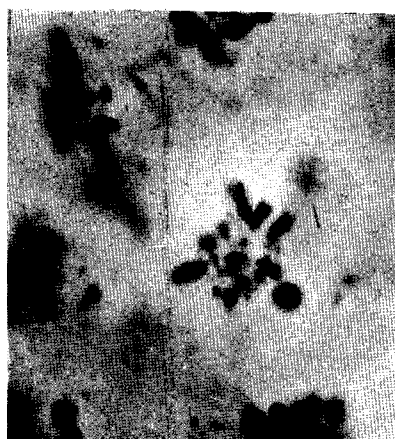
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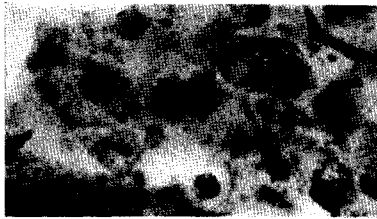
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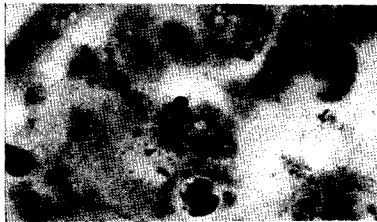
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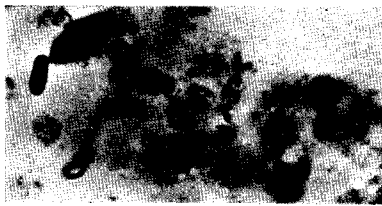
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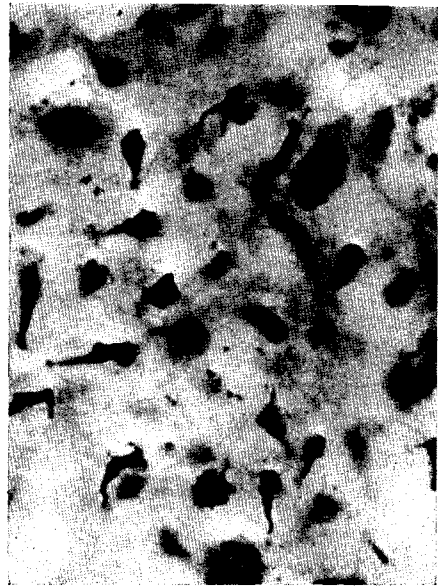
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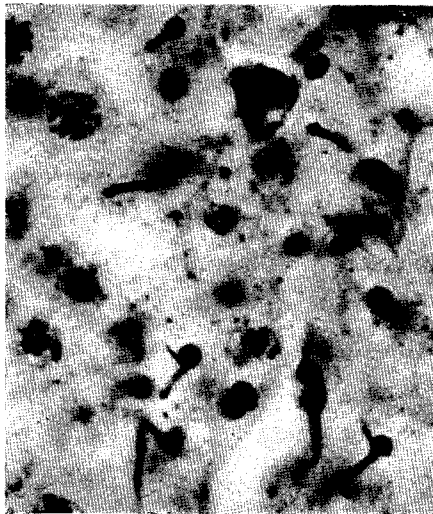
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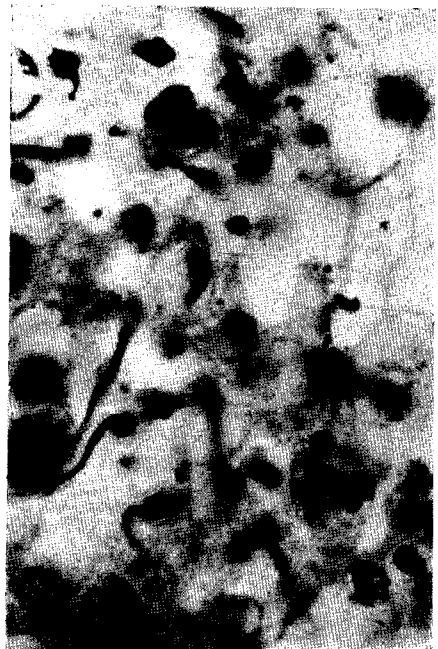
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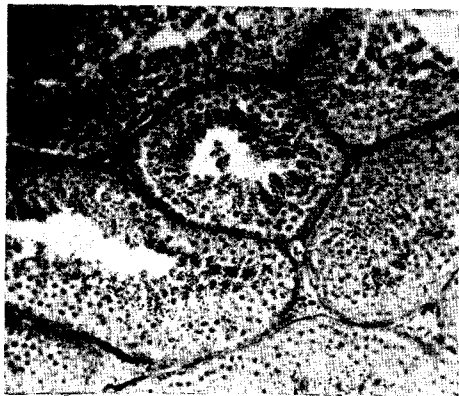
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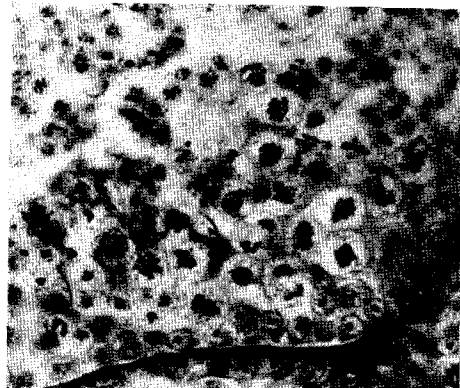
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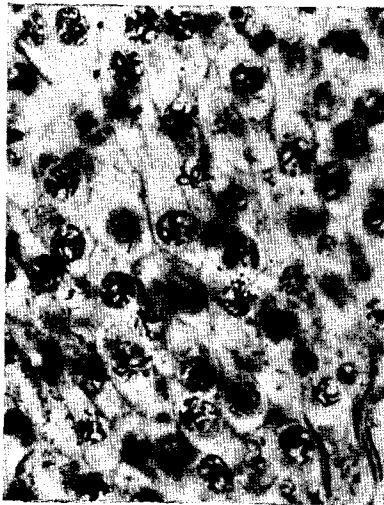
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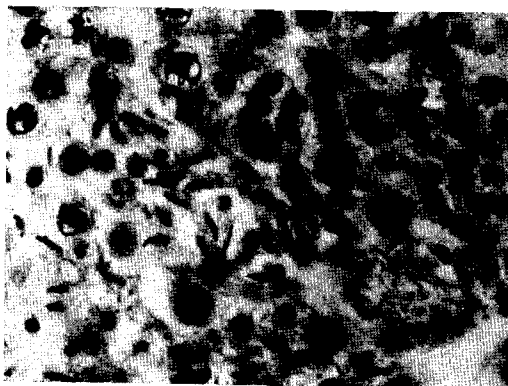
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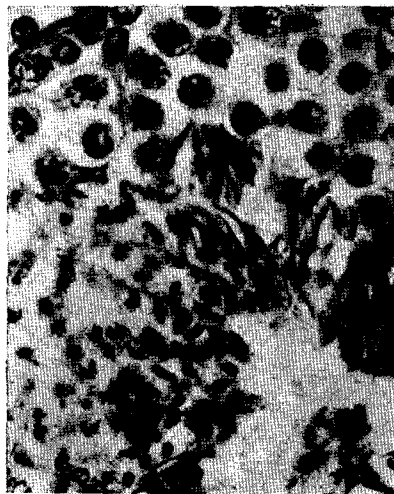
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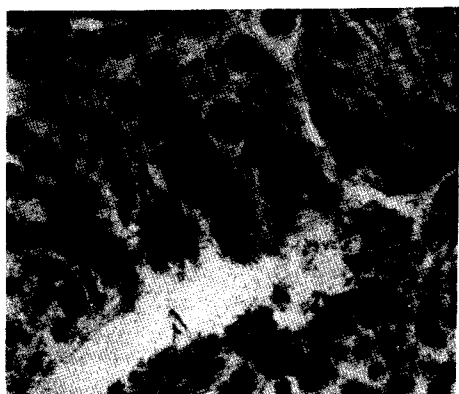
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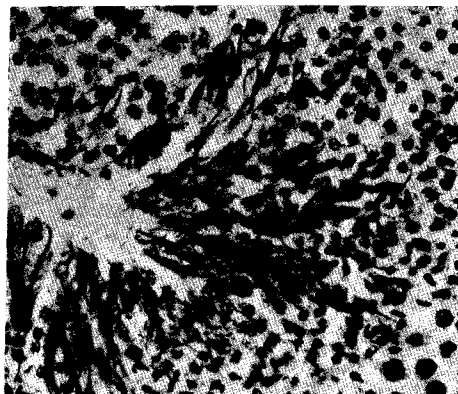
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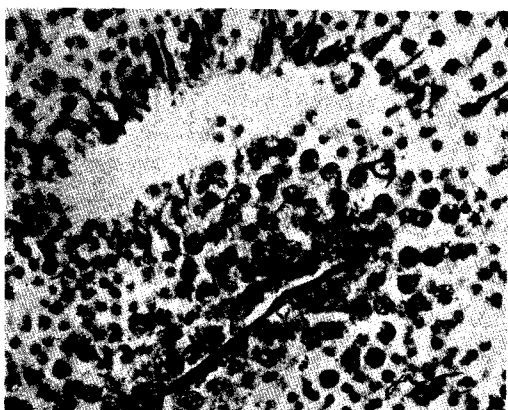
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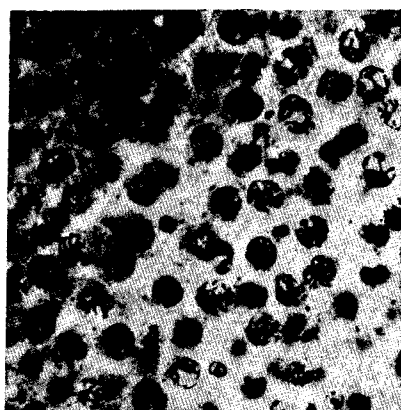
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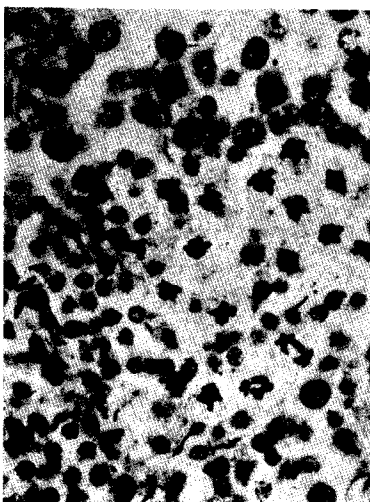
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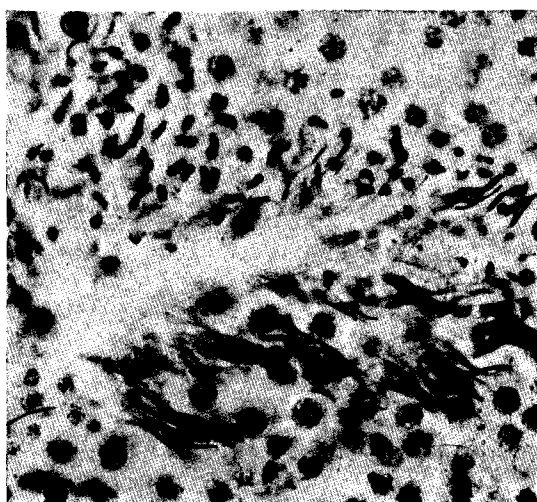
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