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Studies on Sauropsid Chromosomes
IV. Chromosome Numbers of Sea-Birds New to Cytology¹⁾

By

Kan Oguma

Zoological Institute, Hokkaido Imperial University, Sapporo

(With Plate VII and 16 Textfigures)

The class Aves, an interesting but difficult field of research, still remains closed for the most part to cytologists, who have already succeeded in the Reptilia, the sister class to the Sauropsida, in grasping the exact knowledge of chromosome morphology. Even in domestic fowls, on which more than twenty investigators have hitherto undertaken studies to explore what characteristics exist in the chromosomes, we still find many unsolved points, not absolutely reconciled in the results of their observation. Turning to the other kinds of birds, it is to be noted that the studies have chiefly been extended to the birds at least partly domesticated under confinement, such as species of pheasants and ducks, and seldom to species of wild birds, due probably to the difficulty of obtaining materials suitable for cytological studies.

Under such circumstances it is really a matter of importance to collect exact data from some other kinds of birds than domestic fowls and ducks in order to elaborate the present incomplete knowledge on Avian chromosomes. The present memoir, based upon a comparative study of chromosomes of wild sea-birds, will suffice to some extent in increasing the scope of knowledge on the Avian chromosomes.

Material and Method

Materials employed in the present study were collected in fields and the sea by random shooting while birds were flying or swimming.

1) Contribution No. 118 from the Zoological Institute, Faculty of Science, Hokkaido Imperial University, Sapporo.

In this respect the studied species are quite different in their taxonomical position from those utilized by most investigators of Avian chromosomes. Under the author's direction Dr. Makino kindly spent a few weeks at Akkeshi, during the summer of 1935, where the Marine Biological Station belonging to our Faculty of Science is situated. Fortunately he succeeded in obtaining as materials specimens of more than ten different species of sea-birds. In a few species, however, it proved that the germ-cells were not in condition suitable for a close investigation of chromosomes, since the dividing activation of cells was waning in their sexual cycle¹.

The dissection of bird bodies and fixation of gonads had necessarily to be accomplished while the heart beating still continued in birds felled by shooting. Otherwise, the chromosomes never show their clear live figures as it was desired to get. The material, therefore, had to be secured from those birds whose wounds were not mortal. When the birds were shot down on fields the dissection and the consequent treatment were carried on right where they fell, while when shot on the sea similar treatments were performed on the motor-boat, from which the hunter fired.

As the collecting place is far north in Japan, the birds thus obtained are chiefly confined to those belonging to the subarctic fauna. But at this opportunity the author wishes to report one more species of gulls obtained in a similar manner at Toyohashi situated in the middle part of Japan, in connection with those collected at Akkeshi. Thus the material of the present study is composed of six species, entirely new to cytology, as enumerated below:

Order Tubinares. (1) *Oceanodroma leucorhoa leucorhoa* Vieillot. (4 males)

Order Steganopodes. (2) *Phalacrocorax carbo hanedae* Kuroda (1 male)

1) For this reason the following four species of sea-birds were unfortunately useless for karyological study, because of shrinkage of testes, in which no dividing cells were contained:

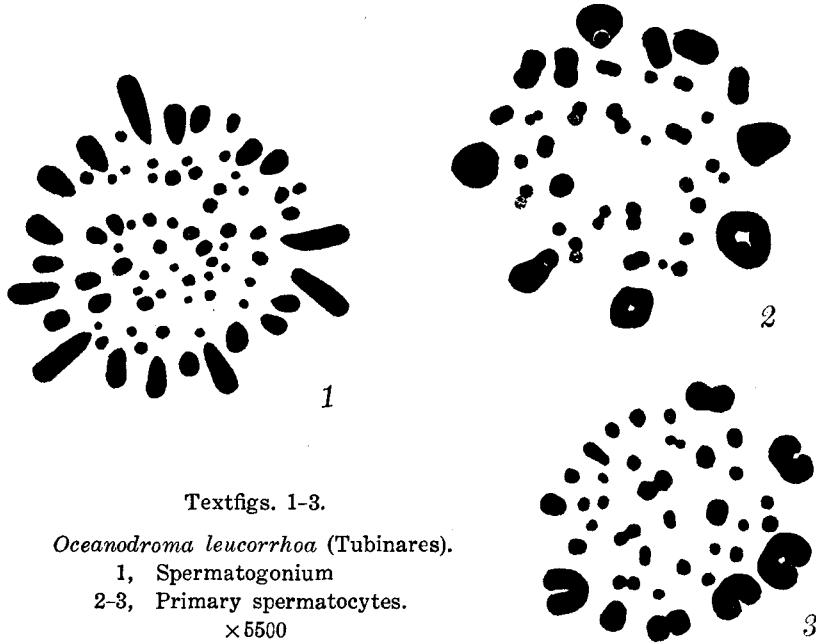
Urile pelagicus pelagicus Pallas.

Uria carbo Pallas.

Mergus merganser merganser L.

Larus crassirostris Vieillot.

This number can be determined in every cell, in which overlapping does not take place among chromosomes. The majority of long rod-shaped ones, at least in ten or eleven pairs, of which two are remarkably long, arrange themselves radially in the metaphase plate, constituting a peripheral circle. The spherules, on the contrary, usually occupy the central area in company with a few pairs of shorter rods.



Textfigs. 1-3.

Oceanodroma leucorhoa (Tubinares).

1, Spermatogonium

2-3, Primary spermatocytes.

×5500

The bivalent chromosomes. In the metaphase plates of the primary spermatocytes (Textfigs. 2 and 3, Figs. 3 and 4 in Pl. VII) 37 bivalent chromosomes are invariably found without the least ambiguity. Corresponding to the preceding case, the larger chromosomes, of which 4 or 5 of the largest category become converted into horizontal ring-tetrads, form the outer circle of the equatorial arrangement of tetrads.

Order Steganopodes

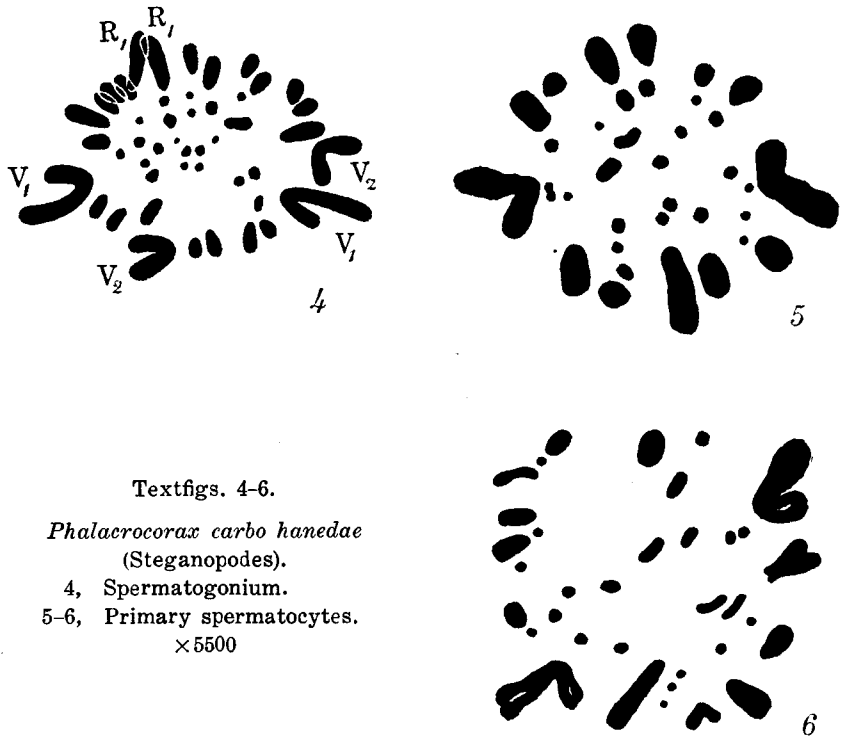
2. *Phalacrocorax carbo hanedae* Kuroda.

Only a single male was available for the present study. Even in this individual the most active stage of the germ-cells was already

passing in their sexual cycle, as the seminiferous tubules very seldom contain spermatogonia in which the division of chromosomes is actually taking place.

The univalent chromosomes. Under such an unfavorable condition, it seems to be quite impossible to determine the chromosome number characteristic to the present taxonomically interesting species of sea-birds. Very fortunately, however, a unique example of a dividing spermatogonium viewed from the pole of division was discovered. Textfig. 4 shows the chromosomes of that cell. In the peripheral zone of the equatorial plate are arranged the larger chromosomes, which surround the smaller ones, of which a number of the smallest ones or spherules evidently become invisible by bleaching. This is the principal reason why it was impossible to determine the chromosome number in this case. The discussion of morphology of chromosomes will therefore be based upon those of larger size, which are well stained and therefore can be compared with the corresponding ones of other species. Two pairs of huge V-shaped chromosomes show a striking configuration among the smaller ones of rod-shape. Particularly, one pair of such V's (V_1) is evidently characterized by their superior size with two component arms of unequal length. Another pair of V's (V_2) seems to have arms essentially dissimilar with each other, as supposed from the morphology of their bivalent condition (*vide infra*) in spite of the apparently typical V-shape with equal arms, of which the longer one becomes shortened in projection because of its oblique position in the metaphase plate. There are found no more V's, in striking contrast to all normal cases known from the Avian group, as far as the present single case is concerned, but it seems better to postpone a definite conclusion until further study may have been undertaken again with abundant material.

The bivalent chromosomes. In more than ten different slides the dividing primary spermatocytes are found in which the bivalent chromosomes are discovered in a definite number. The number of chromosomes of such reduced condition is constantly 35, from this number the diploid number may theoretically be supposed 70. Two of the best preserved metaphase plates are reproduced in Textfigs. 5 (= Fig. 5 in Pl. VII) and 6 (= Fig. 6 in Pl. VII), in which two atelomitic chromosomes are readily distinguishable as the descendants of V's found already in the spermatogonium with correspond-



Textfigs. 4-6.

Phalacrocorax carbo hanedae
(Steganopodes).

4, Spermatogonium.
5-6, Primary spermatocytes.
× 5500

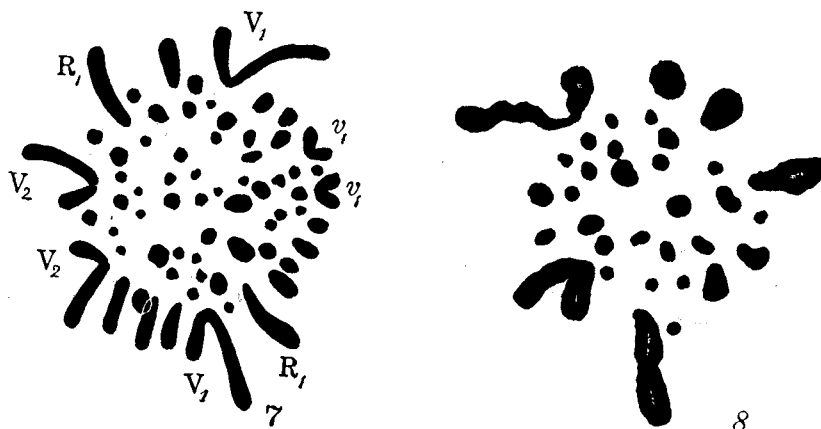
ing configuration. They appear like J's having dissimilar arms with more than two chiasmata in the longer components. The remaining 31 are represented by rods with gradatory reduction of length until they become spherules; 13 of the longer ones constitute the peripheral zone in their metaphase arrangement.

Order Lari

3. *Sternula albifrons sinensis* Gmelin.

The univalent chromosomes. The studied testes showed a very good condition so far as the chromosomes are concerned, involving a great many dividing figures of the spermatogonia as well as the primary spermatocytes, both of them being quite well fixed. A spermatogonium comprises without exception 66 univalent chromosomes (Textfig. 7 and Fig. 7 in Pl. VII), of which 12 (in 6 pairs) seem to constitute the macro- or M-chromosomes arranged in the peripheral

zone of metaphase plate, enclosing the remaining micro- or m-chromosomes within. Two pairs of the largest and the second largest ones (V_1 and V_2) among M-chromosomes closely resemble each other in their configuration, as all show V-shape with arms of different length. In addition to these 4 large V's, there exists one more pair of small V's (v_1) with approximately equal arms. The remaining 6



Textfigs. 7-8. *Sternula albifrons sinensis* (Lari). 7, Spermatogonium
8, Primary spermatocyte. $\times 5500$

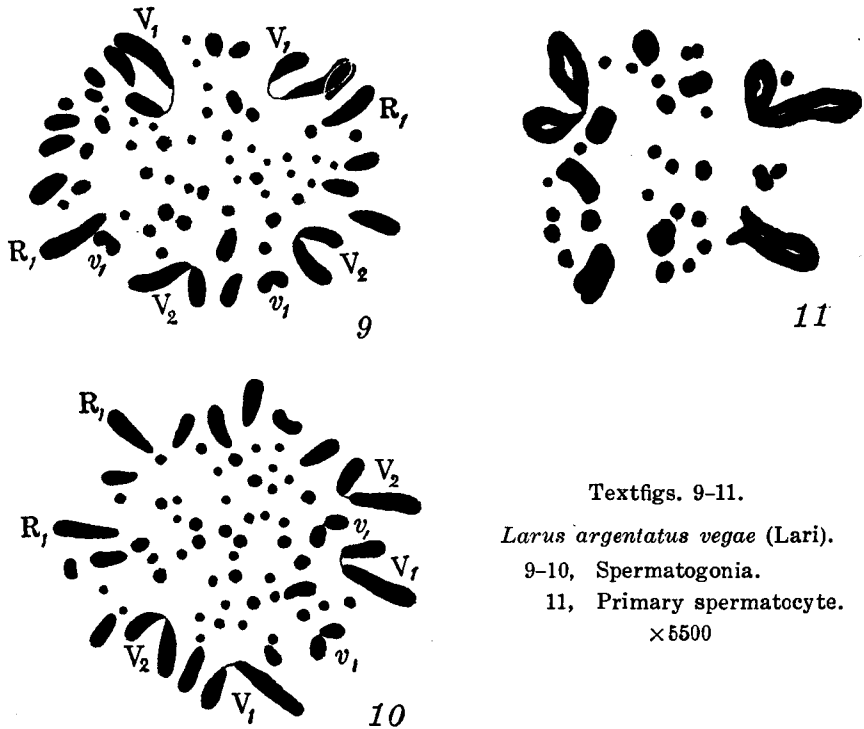
M-chromosomes are typical rod-chromosomes having telomitic fibre attachment. The small, micro- or m-chromosomes enclosed by M-chromosomes in an equatorial plate are 54 (27 pairs) in number. They reduce their length showing gradation from short rods, of which a few pairs are scarcely distinguishable from the shortest ones of the M-chromosomes, up to complete spherules.

The bivalent chromosomes. In the metaphase plate of the primary spermatocyte are always found 33 bivalent chromosomes (Textfig. 8; Figs. 8 and 9 in Pl. VII) descended from 66 univalents of the spermatogonium. The 6 M-bivalents can readily be identified by their large size as well as their relative position on the equatorial plate, but unfortunately it is obscure at present which one may be the descendant of the small V's (v_1) conjugated into one bivalent.

4. *Larus argentatus vegae* Palmén

The univalent chromosomes. In this species of gulls, the distinction between macro- and micro-chromosomes becomes more con-

spicuous as compared with the preceding species (Textfigs. 9 and 10; Figs. 10 and 11 in Pl. VII). This shows an intergeneric or an interspecific difference of chromosomes between the present and the preceding gulls. The total number of chromosomes as determined by counting in five cells is 66, in agreement with the former species. These 66 univalents are easily divided into 18 large M-chromosomes



and 48 small m-chromosomes, the former constituting the outer circle, within which the latter are evenly scattered. The largest and the second largest pairs of M-chromosomes are V's with arms of unequal length. There are also found two small V's (v_1) having arms of equal length in addition to the two pairs of large V's (V_1 and V_2). In this respect, therefore, the present species is quite similar to the preceding one, but all these three pairs of V's have a marked characteristic in distinction from all species dealt with in this study. That is the strong tendency of constricting off of the component arms at

the apex of the V-shape. In an extreme case one may sometimes consider one chromosome as if it were two distinct chromosomes (notice the largest pair in Textfigs. 9 and 10).

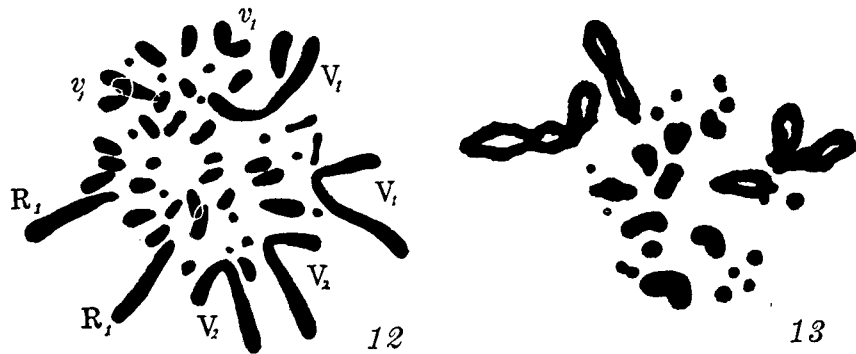
The m-chromosomes, 48 in number, are for the most part spherules, including a few pairs of short rods, which are still distinguishable from the shortest M-chromosomes.

The bivalent chromosomes. The primary spermatocyte contains 33 bivalent chromosomes as shown in Textfig. 11 and Fig. 12, Pl. VII. In such a haploid garniture of chromosomes the corresponding ones of 9 pairs of M-chromosomes are readily distinguishable by their remarkably large size (Textfig. 11 and Fig. 12 in Pl. VII). The largest two pairs of V-univalents transform themselves by conjugation into two largest bivalents with the structure of compound ring-tetrads, but the small V's (v_1) conjugated, seem to retain their original V-shape after conjugation (top, right-hand in Fig. 12, Pl. VII), of which the arms may sometimes open widely (middle, left-hand in Textfig. 11).

Order Alcae

5. *Brachyramphus marmoratus perdix* Pallas

The univalent chromosomes. The testes employed for the study did not contain the dividing spermatogonia in desirable number, since merely two equatorial plates, favorable to observation of the complete set of component chromosomes, could be discovered from the slides. The chromosome number seems with all probability to be 50 since in both of these two cases the same number was countable. A glance at Textfig. 12 (= Fig. 13 in Pl. VII) will note the 3 large pairs, of which two are V's (V_1 and V_2) and the remaining one, rods (R_1). They acquire extremely huge size as compared with the remaining shorter chromosomes; the longest rods (R_1 in Textfig. 12) for instance, attain about three times the length of the second longest rods. There is also present one more pair of V's of smaller size (v_1), possessing two arms of equal length, in addition to the large V's with dissimilar arms. Referring to the bivalent chromosomes (*vide infra*), there may occur probably two additional pairs of small V's among the univalents, but unfortunately the point still remains uncertain because of the insufficient number of cases actually observed.



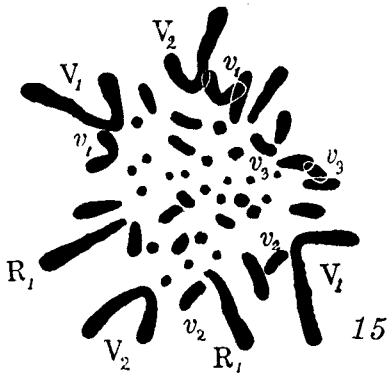
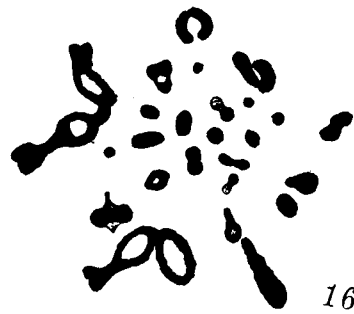
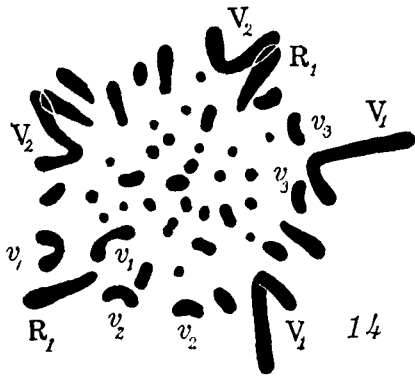
Textfigs. 12-13. *Brachyramphus marmoratus* (Alcae).
 12, Spermatogonium. 13, Primary spermatocyte.
 ×5500

The bivalent chromosomes. The number of bivalents is constantly counted as 25, at least in 3 metaphase plates of the primary spermatocytes of the best fixation, as in one of them shown in Textfig. 13. The largest three, two of them being atelomitic, are evidently accounted for as the descendants of three pairs of univalents of extremely large size. Beside these 3 bivalents, 9 more probably belong to the M-chromosomes, considered from their relative magnitudes in contradistinction to the remaining 13 bivalents of spherular form. Among these 12 apparent M-chromosomes, are included three small V-tetrads (Textfig. 13), of which the one (bottom in middle) may certainly represent the conjugated small V's (v_1), but as for the remaining two their form previous to conjugation is uncertain.

6. *Lunda cirrhata* Pallas

The univalent chromosomes. The present species possessed testes containing cells in very favorable condition in their sexual cycle for karyological study, as many dividing figures were discovered in spermatogonial cells as well as in the primary spermatocytes. The univalent garniture of chromosomes is certainly made up of 50 distinct ones, similar to the preceding species (Textfigs. 14 and 15; Figs. 14 and 15 in Pl. VII). The chromosomes constituting the peripheral zone of a metaphase plate fluctuate in number from 20 to 22 and they are presumed to be M-chromosomes, among which two pairs of large V's (V_1 and V_2) are as prominent as those of the preceding

species in respect to size and form but the pair of longest R's (R_1) seems much shortened. The small V's (v_1) with arms of approximately equal length are also found with the similar configuration to the other cases of Avian chromosomes. Closer observations reveal, however, that there seem to exist two more pairs of smaller V's (v_2 and v_3) in addition to v_1 's, considered from their mode of arrangement on the equator, although they are not assuming the typical V-shape with sharp apices. If this be true, the presence of three pairs



Textfigs. 14-16.

Lunda cirrhata (Alcae).

14-15, Spermatogonia.

16, Primary spermatocyte.

× 5500

of small v 's should be the common characteristic between species of the Order Alcae, since in the preceding species their occurrence may probably be expected, as mentioned already. The distinction between macro- and micro-chromosomes is not marked as there are many rod-chromosomes of intergrading magnitude.

The bivalent chromosomes. In the primary spermatocyte 25 bivalent chromosomes can be easily counted as shown in Textfig. 16

(= Fig. 16 in Pl. VII). The largest 3 chromosomes, the descendants of V_1 , V_2 and R_1 , are readily discriminable, but the small V's (v 's) could not be identified with certainty except the v_1 (top, right-hand).

General Consideration

From what has actually been observed in chromosomes of the wild sea-birds now dealt with, it seems not difficult to conclude (1) that the chromosome number is not variable but constant in every one and the same species, (2) that there exist some morphological characteristics, common to different species belonging not only to the same order but also to different orders, and (3) that in certain cases the chromosomes show little resemblance in morphology with ordinary cases.

Constancy of the chromosome number. In his previous paper on chromosomes of the pigeon, the present author came first to the conclusion that the minute chromosomes, spherical in shape and occupying the central region of the equatorial plate, are as constant in their number as those of the long rod-shape or V-shape, having the same ponderance with the latter in respect to their individualities. Such minute spherules, however, exhibit a strong tendency to become obscure to our vision by rapid fading of stain when bleaching advances a little too far, owing probably to their minute volumes. It is for this reason, in the most part of cases, why the variation of chromosome numbers has been so frequently recorded from one and the same species as the domestic fowls for instance. From this kind of bird, on which 25 different studies have been published by 20 authors, such as Loyez (1906), Sonnenbrodt (1908), Lécaillon (1910), Guyer (1909, 1916), Cutler (1918), Boring (1923), Hance (1923, 1924, 1925, 1926a, 1926b, 1926c), Shiwago (1924), Akkeringa (1927), Goldsmith (1928), Suzuki (1930), Kemp (1930), Saguchi (1930), White (1932), Popoff (1933), Sokolow and Trofimow (1933), Sokolow, Tiniakow & Trofimow (1936a, 1936b) and Unger (1936), it seems hardly possible determine the definitive chromosome number. It may sometimes depend actually on the variable nature of the chromosomes if the cells studied so far belong to somatic cells, since the similar occurrence has often been informed from other kinds of animals like mammals; still there remain doubts whether such spherules have been observed accurately as they really exist.

Among many contributions notice may be paid to only these three, by Suzuki (1930), White (1932), and Unger (1936), who report the chromosome number of the domestic fowl from observation of the germ-cells. The first was the favoured author who established the constant chromosome numbers 74 in the spermatogonium, 37 in the primary spermatocyte and 73 in the oogonium, while the latter two were not successful in obtaining a constant number but fluctuating numbers. In addition to the above three cases in *Gallus domesticus*, the germ-cells have also been employed for research in relation to chromosomes in *Turdus merula* and *Linota cannabina* by Unger (1936), *Melopsittacus undulatus* by Jentsch (1935), *Anas platyrhynchos* by Werner (1925, 1927), *Columba livia* by Oguma (1927), *Phasianus colchicus* by Trofimow & Tiniakow (1933), *Phasianus torquatus* by Unger (1936), and *Meleagris gallopavo* by Werner (1931), but the definitive number of chromosomes was reported only in the case of the pigeon by Oguma (1927), the turkey by Werner (1931) and of the zebra parrakeet by Jentsch (1935). It is quite noteworthy that the latter two authors informed the constancy of the chromosome number not only in germ-cells but also in somatic cells as amnion, in which have frequently been reported the variable numbers in various species of birds.

Particularly the results of Jentsch (1935) obtained from the study of the zebra parrakeet, *Melopsittacus undulatus*, are strikingly clear in proving the occurrence of a constant number of chromosomes, of which all 44 representatives, minute spherules inclusive, can be found with their characteristic form and size in every cell of the amnion he examined. This fact strongly emphasizes the view that the chromosome number is not variable even in somatic cells in ordinary cases and that, at the same time, the reported fluctuation of the chromosome number in one and the same species of birds is not an actual occurrence but merely depends on how many spherules out of the whole have actually been subjected to count by different authors. In ideal preparations, so far as the experiences of the present author show, the minute spherules are always found constant in number, similar to the remaining larger chromosomes, showing consequently no numerical variations. Under such circumstances the present results obtained from six different species of sea-birds should be considered very important, since in all six species the characteristic chromosome numbers could be determined.

Comparative morphology of chromosomes. Comparing the chromosomes in the six studied species, it is extraordinarily clear that *Oceanodroma leucorhoa* presents a quite strange feature by possessing no V's, which are so universally discovered not only in the remaining five species under the present investigation but also in all other species belonging to the class Aves hitherto reported by previous authors. The 74 chromosomes invariably take rod-shape to be designated by R's and this chromosome number coincides with that of *Gallus domesticus* determined by Suzuki (1930), irrespective of their taxonomical relation.

We know at present that such a garniture of chromosome, composed of only one kind of R's, is found in Sauropsida merely in some Reptilia, as in species of Lacertidae (Matthey, 1931; Nakamura, 1931, 1935; Oguma, 1934), some belonging to Geckonidae (Nakamura, 1932; Matthey 1931) and in *Japarula swinhonis* of Agamidae (Nakamura, 1931, 1935). It is of great importance that, in chromosomes, the order Tubinares shows allied morphology to Reptilia rather than to Aves, and this will present at the same time the primitive feature of the chromosomes in parallel to their taxonomical position of Tubinares in ornithology.

The remaining five species, different in the orders to which they belong, have similarly a number of V's as constant components of the definite garniture of chromosomes. These V-shaped chromosomes can be divided into two different types. One belongs to the largest chromosomes, their component two arms being remarkably different in length; the other acquires a medium size with two arms of approximately equal length. The former ones are better distinguished by designation as V_1 and V_2 from the latter ones which are indicated by v_1 and v_2 according to their gradation of size.

The V_1 and V_2 are unexceptionally present in all five species included in Steganopodes, Lari and Alcae. A similar occurrence is known not only in major cases of Carinatae but also in the species of Ratitae as Shiwago (1936) recently explored their existence, but the v 's are quite different from the former in respect to actual number in existence. In a majority of cases v_1 's are found in a pair, like the case of the domestic fowl, *Gallus domesticus*, as reported by Suzuki (1930), Sokolow & Trofimov (1933) and Sokolow, Tiniakow & Trofimov (1936a & 1936b), and this pair of v_1 has been considered at the same time as the X-chromosome by the above authors.

In *Phalacrocorax carbo hanedae* of Steganopodes the present author could not identify them with certainty in a single observed case of the spermatogonium. However, the occurrence of such a chromosome garniture destitute of *v*'s as in the above species seems of no particular significance in members of the Avian class, because in the Lamellirostores Russian investigators have recently reported similar cases as in *Anas platyrhyncha* and *Carina moschata* by Sokolowskaja (1935) and in *Anas boschas* by Alichanian (1936).

The supernumerary *v*'s were merely found in members of the order Alcae, as *Lunda cirrhata* and probably *Brachyramphus marmoratus perdix*, in which v_2 and v_3 are to be placed after v_1 's. Analogous composition of chromosomes seems to exist, as the present author believes, in some other kind of birds such as the ring-dove, *Streptopelia risoria*, now under investigation. As the reported evidences, the three species of Gallinaceae, *Pavo cristatus* (peacock), *Numida meleagris* (guinea fowl) and *Tetrao tetrix* (woodcock), may be enumerated here as the possessors of v_2 's (v_3 absent) from the combined work of Sokolow, Tiniakow and Trofimov (1936).

The following tabulation¹⁾ explains in brief the chromosome relations as found in the six species of sea-birds now investigated.

Order	Species	2n	Formula
Tubinares	<i>Oceanodroma leucorhoa</i>	74	74 R's
Steganopodes	<i>Phalacrocorax carbo</i>	70	66 R's+4 V's
Lari	<i>Sternula albifrons</i>	66	60 R's+4 V's+2 v's
—	<i>Larus argentatus</i>	66	60 R's+4 V's+2 v's
Alcae	<i>Brachyramphus marmoratus</i>	50	40 R's+4 V's+6 v's
—	<i>Lunda cirrhata</i>	50	40 R's+4 V's+6 v's

From the data briefly set down in the above tabulation the conclusions under three topics are to be brought forth without difficulty:

1. The chromosome number decreases when V-chromosomes increase their number; the Tubinares, in which V's are entirely absent, shows the highest number as 74, and this number reduces in

1) In the second column the subspecific names are omitted. In the fourth column, R = Rod-chromosome including spherules, V = large V-chromosome and *v* = small V-chromosome.

gradatory manner to 70 in the Steganopodes having 4 V's, 66 in the Lari possessing 6 V's and at last into 50 in the Alcae with ten V's.

2. The chromosomes seem to be constant in different species of one definite order, as in the 66 chromosomes similarly found in both species of the Lari and 50 ones in either species of the Alcae.

3. It seems impossible to discover any fundamental number of chromosomes by means of analysing two component arms of one V into two R's, except in one case of Steganopodes. In fact the Japanese cormorant, *Phalacrocorax carbo hanedae*, of that order possesses only two pairs of V's among the whole 70 chromosomes, and if these 4 V's are analysed into 8 R's then the chromosome number will become 74, similar to *Oceanodroma leucorhoa* of the Tubinares. But the present author doubts at present whether such manner of chromosome analysis is correctly applicable and whether it has any significance between these two different kinds of birds.

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Explanation of Plate VII

Photomicrographs of chromosomes of the sea-birds, taken under magnification $\times 2000$.

Oceanodroma leucorhoa leucorhoa (Figs. 1-4).

- Figs. 1 and 2. Spermatogonia; Fig. 1 corresponding to Textfig. 1.
- Figs. 3 and 4. Primary spermatocytes, corresponding to Textfigs. 2 and 3 respectively.

Phalacrocorax carbo hanedae (Figs. 5 and 6)

- Figs. 5 and 6. Primary spermatocytes, corresponding to Textfigs. 5 and 6 respectively.

Sternula albifrons sinensis (Figs. 7-9)

- Fig. 7. Spermatogonium, corresponding to Textfig. 7.
- Figs. 8 and 9. Primary spermatocytes; Fig. 8 corresponding to Textfig. 8.

Larus argentatus vegae (Figs. 10-12)

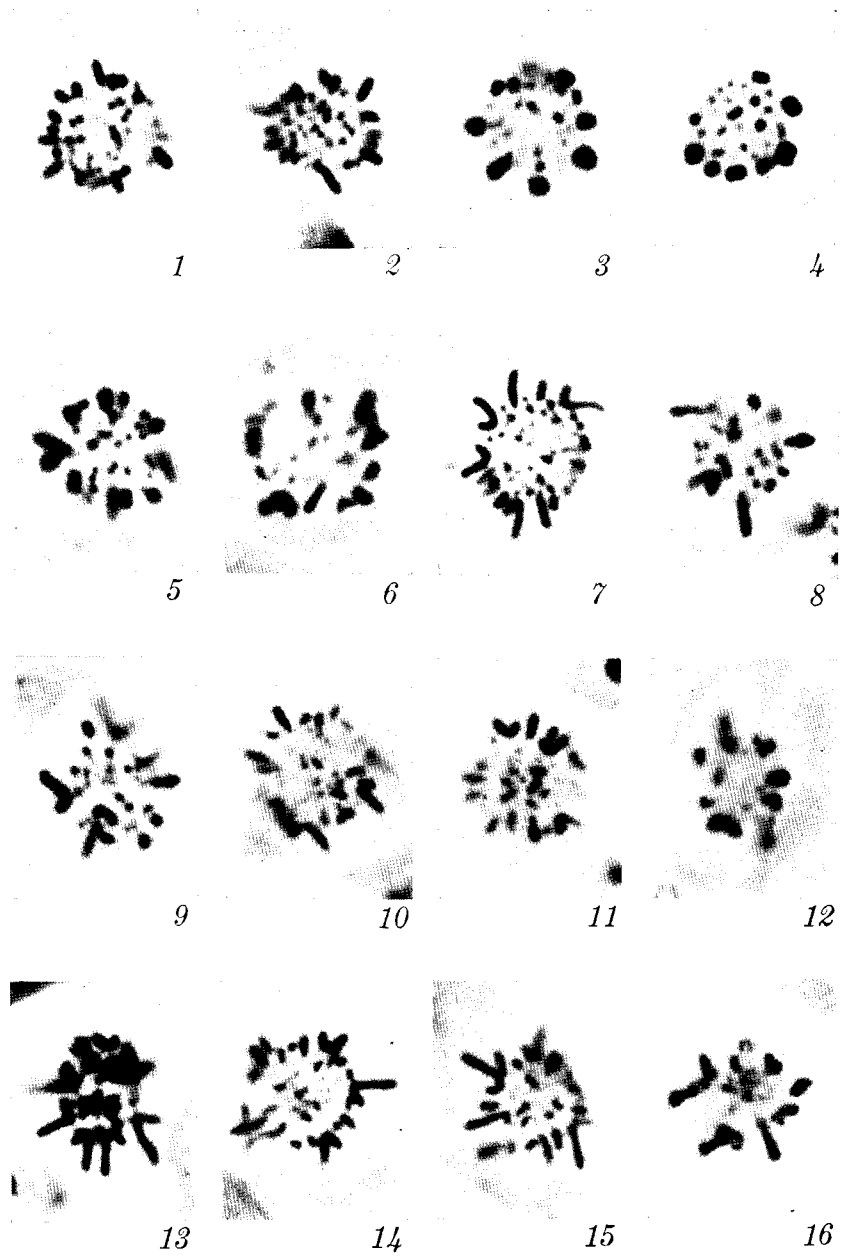
- Figs. 10 and 11. Spermatogonia; Fig. 10 corresponding to Textfig. 10.
- Fig. 12. Primary spermatocyte.

Brachyramphus marmoratus perdix (Fig. 13)

- Fig. 13. Spermatogonium, corresponding to Textfig. 12.

Lunda cirrhata (Figs. 14-16)

- Figs. 14 and 15. Spermatogonia, corresponding to Textfigs. 14 and 15 respectively.
- Fig. 16. Primary spermatocyte, corresponding to Textfig. 16.



K. Oguma photo.