PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

On Dimensions of Chromosomes Considered in Relation to Phylogeny

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PHILOSOPHICAL TRANSACTIONS.

I. *On Dimensions of Chromosomes considered in Relation to Phylogeny.*

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[Plates 1 and 2.]

Cytologists are very generally agreed that a correspondence, more or less definite, exists between the size of the nucleus and that of the cell in which it is present. Strasburger, Gerassimow, Hertwig, Nemec and others have laid special stress on this relation, and it has been used as the basis for speculation and experiment on the inter-relation of the cytoplasm and nucleus. Strasburger, in 1893, as the result of a number of careful estimations, concluded that in young and active cells the ratio of the volumes nucleus/cell commonly approximates to 2/3. But obviously this relation can no longer hold good when the cell has so far increased in size that large sap vacuoles have come to occupy a considerable part of its total volume. Hertwig gave additional precision to the idea in formulating his well-known Kern-plasma relation. He selected as his two units the volume of the nucleus and that of the cytoplasm, instead of the nucleus and total cell dimension.

A considerable amount of experimental work has shown that Hertwig's view accords fairly closely with the results of observation and experiment and the researches of Nemec in particular are valuable in this connection. This investigator showed that by the use of chloral hydrate the cell wall normally formed between two dividing nuclei could be prevented from forming, and that failure to isolate the two cells by the partition wall was sometimes followed by a re-fusion of the nuclei to form a specially large one. The progeny of such a cell continued to manifest the qualities of gigantism, and the large nuclei, and correspondingly large cells, could easily be recognised in the tissues which had undergone the chloral hydrate treatment indicated above. Observations made by Miss H. Kemp in London only served to confirm Nemec's statements on this point.

Again the same kind of proportion is maintained between the cells of the two varieties of *Ascaris megalocephala*, in one of which (var. *univalens*) the nuclei and the cells are smaller than in the more common variety known as *bivalens*.

Many other similar instances could be quoted, *e.g.* the aposporous mosses investigated by Él. and É. Marchal, but perhaps no useful object would be served by further multiplying examples.

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It is, however, a question of considerable interest whether the proportional relationship so commonly observed to subsist between nuclear and cytoplasmic dimension is one of size and of quality of substance only, or whether it can be further linked up with any morphological structure such as the chromosomes, which have by many people been supposed to underlie, and to be responsible for, the hereditary qualities of the organism. An enquiry of this sort is the more needed at the present time, inasmuch as conclusions of a far-reaching character concerning relations supposed to exist between certain chromosomal dimensions and phylogeny have recently been arrived at by Captain Meek, in a memoir which appears in the 'Philosophical Transactions' of this Society. It is therein stated that the widths of chromosomes are successively greater in higher zoological phyla, and that this dimension is constant for very large groups of animals—for the whole of the higher Metazoa, including and above the Nemathelminthia, for example. We shall refer at greater length to Captain Meek's work later on. It is sufficient at this stage to call attention to it.

We have deemed it desirable to ascertain :—(1) How far the chromosomes may be taken as an indication which can be safely utilised, even within narrow limits of affinity, for the purposes of the Kern-plasma (K/P) relation. (2) How far a comparison of their volumes in related forms may serve to throw light on certain as yet unsolved problems of nuclear constitution in cases like that of the Primula hybrids and Œnothera mutants, in which they are sometimes present in twice the number that would have been anticipated. (3) We have also been led to examine a number of animals and plants in order to satisfy ourselves as to whether the important generalisations of Meek are or are not well founded.

Although, from a theoretical point of view, the K/P relation of Hertwig is a better ratio than nucleus/cell dimension formula, the latter is of course much easier to arrive at, and if the question is one of comparison between the observed ratios in the cells of similar organs no great error will be introduced provided the observations are made on young cells, *i.e.* on those in which the large sap vacuoles have as yet not appeared.

In the case of the two varieties of Ascaris, alluded to above, the ratio is fairly accurately maintained, and furthermore there is a tolerably close correspondence between the size of the nuclei and the number of the chromosomes. In other words, the chromatic content of the small nuclei of the variety *univalens* is about half (or even less) that of the larger variety and this accords with the respective number of the chromosomes in these two varieties.

But the correspondence as regards number is not nearly so close in a group of varieties of the Lady Fern (*Athyrium Filix-fœmina*) which we have investigated. For this purpose we measured the young epidermal cells of the typical fern and three of its varieties, and in the annexed table we give the size of the cells and the number of the chromosomes respectively.

	Athyrium Filix-fœmina (type).	*Ath. F.-f.*, var. *clarissima* of BOLTON.	*Ath. F.-f.*, var. *clarissima* of JONES.	*Ath. F.-f.*, var. *Unco-glomerata.*
Size of young epidermal cells . .	100	110	180	200
Number of chromosomes . . .	76	84	90	100

The sizes of the cells are estimated in units, taking the typical form as 100. It will be noted that, although the correspondence is not very exact, the plants fall into two groups, in one of which the proportion of chromosomes to the size of the cells is approximately 76/100, and in the other it is 50/100. It is of some interest to find that the two *clarissima* forms, which were independently raised, belong to different categories, as thus defined. But if we take STRASBURGER'S ratio, *i.e.* nucleus/cell dimension, we find the value $\frac{2}{3}$, assigned by him as the common one, holds good for all the four plants now under consideration. There is, then, no constant relation between the K/P relation and the number of chromosomes present in the nuclei of these ferns.

But whilst in the foregoing series an increase in cell-size was accompanied by an increase (though not in equal proportion) of the chromosomes, no such relation was found to exist when another fern and its varieties was examined. The species selected was *Aspidium Filix-mas*, and its variety *Polydactyla*, of which there are two forms, raised respectively by WILLS and DADDS. As before, the value of the size of the epidermal cells of the type is taken as 100.

	Aspidium Filix-mas (type).	*A. F.-m.*, var. *Polydactyla*, Wills.	*A. F.-m.*, var. *Polydactyla*, Dadds.
Size of epidermal cells	100	90	100
Number of chromosomes.	144	132	130

The ferns above mentioned were not suitable for the measurement of individual chromosomes, owing to their large numbers, and it might, perhaps, be argued that the obvious lack of correspondence in numbers might be compensated by a corresponding difference in the size of the chromosomes. The matter is worthy of more extended enquiry, especially in the light of the results of measurements we have been able to make in the case of *Primula Kewensis*, a hybrid plant with a remarkable nuclear dimorphism. We can claim for the Primula measurements a somewhat high degree of accuracy, inasmuch as they have been made on material specially favourable from the point of view of the chromosomes.

Primula Kewensis exists in several forms, and, although there is some slight doubt as to the exact mode of origin of the first plant, similar forms have frequently been obtained, and always as hybrids resulting from crossing *P. verticillata* and *P. floribunda*, or varieties of these species.

The first example which was obtained long remained sterile, though, ultimately, fertile seed was obtained from plants which had been vegetatively propagated from it. The hybrid, however, now several times produced afresh, commonly sets seed fairly freely.

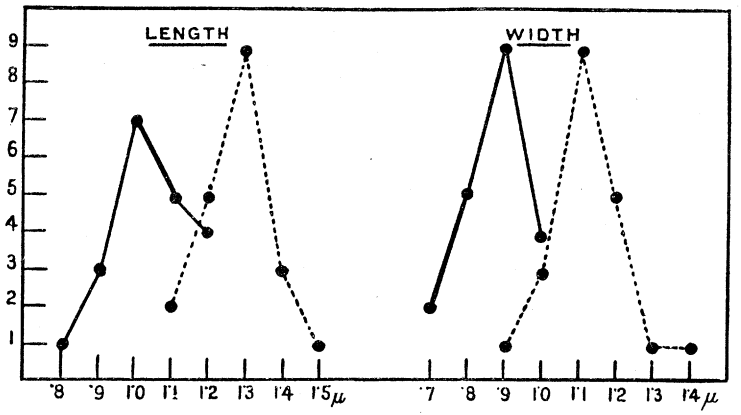
The original example of *P. Kewensis* resembled its parent in having 18 and 9 chromosomes in its premeiotic and postmeiotic nuclei respectively, but the fertile plants which subsequently arose from it—and this is also true of the various more recently obtained hybrids between the original parents (and their varietal forms)—have twice the corresponding number of chromosomes, *i.e.*, 36 and 18. A curious instance has, however, occurred, in which a plant resulting from crossing one of the latter plants (hybrids) back with a parent species has given rise to a form once more possessing 18 and 9 chromosomes.

Careful measurements have, however, furnished what we regard as almost certainly the clue to the peculiar behaviour of these Primula hybrids. In the first place, it became evident that the plants with the larger number of chromosomes possessed nuclei and cells somewhat larger than those of the parents or of the sterile hybrid with the smaller number. The mean of a number of measurements showed that this occurred approximately in the proportion of 5 : 4, a ratio obtained by comparing the volume of the sterile hybrid nuclei (129·3 c.μ) with that of the subsequent seedling hybrids (163·0 c.μ). These volumes were calculated during premeiotic resting stages.

It might, therefore, be anticipated that the larger nuclei, with their numerous chromosomes, would contain a larger amount of chromatin, as estimated by the volume of the chromosomes, than would be present in the smaller nuclei of the sterile hybrid or its parents. Such is not the case. Every care was taken to secure that only those chromosomes were selected with regard to which no doubt as to the accuracy of the measurement could be raised. In all, 20 chromosomes of each class, at early anaphase of the heterotype division, were selected.

The chromosomes are ellipsoidal in form, and it is easy to see that the more numerous chromosomes of the later hybrid are smaller than those of the original plant, with its half number of chromosomes.

The calculation of the total amount of chromatic substance in the nucleus was obtained by estimating the volumes of the ellipsoidal chromosomes at the early anaphase stage (Plate 2, fig. 30) of the heterotype division from the formula $V = \frac{4\pi a^2 b}{3}$, where a = half the width, and b = half the length of the chromosome. As will be seen from the graph, the chromosomes were not constant, either in length or width, although the variations were not considerable.



Primula Kewensis. ——— Later hybrid (36 and 18).
····· Sterile seedling (18 and 9).

The mean of the measurements gave the following results :—

	Average length chromosome.	Average width chromosome.	Volume of each chromosome.	Total chromosome volume in nucleus.
	μ.	μ.	c.μ.	c.μ.
Sterile seedling (18 (and 9) chromosomes)	1·262	1·11	0·8141	14·65
Later hybrid (36 (and 18) chromosomes)	1·022	0·874	0·4088	14·71

Although the above measurements are calculated to the third place of decimals, we cannot attach much importance to estimations beyond 0·1 μ, for not only does the variation in length and width of the chromosomes exceed this amount, but in practice a much greater degree of accuracy than 0·1 μ is not attainable. Nevertheless, the figures as given represent the results of averaging, and it seemed better to leave them as they were arrived at; in any event, they may be taken as the best approximate values we could obtain.

The one fact which does stand out clearly is that the chromosome volumes of the two nuclear types of these Primulas are practically identical, a result which would certainly not have been anticipated from a comparison of the respective sizes of the nuclei.

It is, we think, legitimate to conclude that the doubled number of chromosomes in the later hybrids may be attributed to a transverse fission of the "normal" chromosomes, and not to addition of the chromosomes of a second nucleus, such as seemed at first a not improbable explanation of the double number. The increase of size which accompanies the increase in the number of chromosomes is not at first sight easy to account for, but if it be conceded that the size of the nucleus, and correspondingly the size of the cell, may be correlated with the superficial area of the

chromosomes taken collectively, it is clear that the nuclei of the later hybrids ought to be larger than those of the original hybrid as well as of the parent plant. For on the assumption, which seems to us to be warranted, viz., that each of the original chromosomes has broken transversely so as to give rise to two chromosomes, the added amount of free surface may perhaps be taken as accounting for the increased nuclear and cellular dimension. Such a view accords with the belief, well founded in many instances and perhaps generally true, that the chromosomes do persist as separate entities during the so-called resting stage of the nucleus. Their condition of swelling, commonly though not invariably, renders their individual identification difficult, but these Primulas appear to furnish additional, if indirect, evidence for their independent physiological and structural persistence, even when this cannot be clearly demonstrated in a microscopical preparation.

It would be of great interest to ascertain the conditions obtaining in the possibly analogous case of some *Œnothera* mutants. Dr. R. R. Gates, who has investigated a number of these mutants of *Œ. Lamarckiana*, says of *Œ. gigas*, which contains 28 chromosomes as contrasted with 14 in *Œ. Lamarckiana*, the parent species, that "while in every case the nuclei and cells were undoubtedly larger in *Œ. gigas* than in the corresponding cells of *Œ. Lamarckiana*, yet the ratio varied within wide limits."

It would be very desirable to know to what extent, if any, the ratio of the volumes of the chromosomes in these mutants exhibits variation. It is important to be clear as to the independence of mere size of nucleus as regards its chromosome contents, for it is quite certain that nuclei may vary considerably in bulk, both in different parts of the same organism and in different species, without a corresponding alteration in the dimensions of the chromosomes. The considerable size of the nuclei so characteristic of many parasitic plants is often entirely unrelated to the occurrence of specially large chromosomes, nor does it involve a broad equatorial chromosome figure (*i.e.*, one containing many chromosomes) at metaphase. What may perhaps be designated as the trophic condition of the nucleus does not, then, necessarily afford a reliable indication of the amount of chromatin actually present within it, though it may well be determined by the accumulation of other substances related to, or derived from, the chromosomes.

On the other hand, we cannot disregard the effects which external conditions may sometimes exert on the chromosomes themselves. R. Hertwig, when experimenting on the reaction of developing embryos of *Strongylocentrotus lividus* to high and low temperatures, discovered the important fact that the chromosomes of cells which were produced at low temperatures might be two or three times larger than those formed under warmer conditions. Probably this difference is to be attributed to the more rapid succession of mitoses at the higher temperature, and the consequent curtailment of opportunity for growth on the part of the chromosomes. Morse (1909) also drew attention to the fact that, during spermatogenesis in the

cockroach (*Periplaneta Americana*), the dimensions of the nuclei and of the chromosomes are larger in the earlier than they are in the later spermatogonial divisions.

Conklin (1912) compared the size of the chromosomes in the macromeres and micromeres of *Crepidula*, and states "it is plain from the figures that the chromosomes from the larger nuclei are larger than those from the smaller ones, though the difference in the diameter and volumes of the chromosomes is not so great as the difference in the volume of the nuclei from which they came." He adds, "just as the size of the nucleus is connected with the volume of the cytoplasm in which it lies, so the size of the chromosomes is connected with the volume of the nucleus from which they came." This last cannot, however, be regarded as of general validity; for instance, the Primulas described above could hardly be brought into line with it. Conklin also considers that nutritive conditions, such as are supplied by the surrounding cytoplasm, have a direct influence on the size of the chromosomes. He finds that these bodies are smaller in the spermatid than in the corresponding oötid, but that by the time the first cleavage occurs the two sets of maternally and paternally derived chromosomes are similar in size. He attributes this to the circumstance that "both grow, after fertilisation, in the same medium, the egg plasma, and for approximately the same length of time." This explanation, however, appears to be incomplete, inasmuch as it ignores the initial difference in size. It is not immediately obvious why the initial disparity should disappear at all.

We think the observations of our own detailed above, taken together with those of other observers, support the contention that the chromosomes possess an individuality of their own, and that they do not merely represent discrete lumps of a common substance. That they may break up into smaller units or be temporarily united into larger ones constitutes no serious objection to this opinion, nor does the fact that their size can be affected by nutritive conditions obtaining within the cell touch the question at all. It merely proves that they, like other living organisms or parts of organisms, may be influenced in various ways by their environment; that they react in various ways to physical stimuli. The remarkable experiments of Boveri, Nemec and others are difficult to explain on any other hypothesis, and we think that the examples of the Primulas may be taken as evidence pointing to the same conclusions. We know of no kind of mechanism which, otherwise, could maintain the relative numbers, sizes, and forms of the chromosomes with such definiteness and constancy, and nearly all the work of recent years has only served to emphasise chromosomal individuality.

Unfortunately we know practically nothing about the phylogeny of chromosomes. No convincing hypothesis has been put forward to explain how these remarkable bodies have become organised, nor how their peculiarities have either been brought into existence or are kept so true for a given species.

A daring speculation as to the origin and phylogenetic development of chromosomes

has been advanced by MEEK in the memoir already referred to. He starts with the assumption that the primitive chromosome stuff existed in granules of definite size, and that by a sort of union or conjugation of these granules, the chromosomes of the higher organisms have been evolved. Much of his suggestion is a merely teleological description of what might have occurred, but he bases his main thesis upon the proposition, which he regards himself as having proved, that the widths of the chromosomes are precisely constant for very large phyla of the animal kingdom.

Now it is evident that if such a proposition can be regarded as conclusively proved, or even well founded, it should mark a considerable advance on our knowledge, and should provide a vantage ground for the attack of a new set of problems.

MEEK'S position is, that among the lowest organisms—the Protozoa—the chromosomes have a constant width of 0·21 μ, and that in the lower and higher Metazoa the widths (excluding the heterotropic chromosomes, when present) are 0·42 μ and 0·83 μ respectively. Anyone who has had much experience in the study of nuclei will perhaps feel hesitation in accepting the validity of these measurements when it is stated (p. 54) that "no difficulty has been experienced in determining these widths, for all phases of mitosis are suitable to such measurements . . ." The last statement is not a little surprising, but MEEK appears to have selected the metaphase condition as the stage giving the best results. No one, probably, would admit that the width of a chromosome remains constant through the earlier phases of mitosis, for the state of aggregation of the linin and chromatin is constantly and successively changing (Plate 2, figs. 25, 32, and 38).

A series of drawings is given (Plate 2, figs. 33–37) of mitoses in the root of *Galtonia candicans* to illustrate stages in the separation of the daughter chromosomes. This series demonstrates the gradual increase in width of the daughter chromosomes from the time that they begin to separate on the equatorial plate (fig. 34) until, as independent units, they approach the spindle poles (fig. 37).

We have restricted our measurements to those stages at which the chromosomes are about to congregate, or are congregating, upon the equatorial plate, and in a few instances to very early anaphase (for these phases are easily recognised, and admit of ready comparison as between the chromosomes of one organism and those of another); nevertheless it is still impossible to eliminate all sources of error. To measure the width of a typical chromosome as it goes on to the spindle is comparatively simple, provided that the chromosome shows no fission in its substance (*e.g. Triton* and *Osmunda*); but if the fission cleaves the spireme segments during prophase it is most difficult to find chromosomes the width measurements of which can be taken as a true index of the typical width of a univalent chromosome. A further complication may arise, as in *Crepis virens*, where not only is there an early fission, but the chromosomes become flattened, prior to the separation of their daughter halves.

But as the matter is one of considerable moment, we have re-investigated a

large amount of material derived from animals and plants in order to ascertain whether, in fact, there is any justification for the assertion that the chromosomes of the higher animals, and incidentally of plants also, do exhibit that degree of constancy in the width of their chromosomes which has been claimed for them.

We may say at once that we do not find the chromosomes of members of a given phylum to possess identical widths as stated by MEEK. It is quite clear, on the other hand, that chromosomes of closely related animals (see the instance of the Prawn and the Lobster, described below) may differ very widely in this respect. As we cannot, therefore, admit the validity of the primary evidence urged in support of his theory of chromosomal evolution, it is not necessary to enter into the theory itself. What we propose to do here is to give an account of our own observations on the dimensions of the chromosomes, first discussing briefly the limits within which the observations themselves can be regarded as being substantially accurate.

It must be remembered that in attempting to measure the width of chromosomes, we are engaging on a problem which is rendered difficult on account of the small size of the objects themselves. MEEK seems to claim accuracy to 0·01 μ, but we do not believe that such a claim can be regarded as well founded. He made a number of careful camera lucida drawings, at a magnification of 3048, and averaged the results thus obtained. We do not know the $\pm$ deviations from the mean finally adopted as the accurate measurement. But it is evident that an error of 0·03 mm. in outlining the chromosomes, or in measuring the widths of the drawing when finished, would vitiate the calculated accuracy of the chromosome width by approximately 0·01 μ. We mention this in order to show that, in our opinion, very little reliance can be placed on the value represented by the second place of decimals, in spite of the fact that the measurements, as given by MEEK, are always exactly the same. Thus, the width of every chromosome of the higher Metazoan nuclei is stated to be precisely 0·83 μ.

We have made repeated measurements of the same individual chromosome under various conditions and at different times and dates, in order to arrive at some knowledge of the limits of personal error in so far as we ourselves were concerned. The results were such as to convince us that we could place very little reliance on estimates carried beyond 0·1 μ. We also experimented on possible differences which might be attributable to different treatment, *e.g.* of fixing and staining, of the material. Somewhat contrary to our anticipation, very little difference could be detected in good preparations, and in any event it was so small as to be swamped by the much larger personal margin of error. The same result was arrived at in testing the effect of light of different wave-length as the source of illumination. The brightness of the light as it affected the eye seemed to be the principal cause of any difference we could observe.

A more serious source of error than these which depend on different physical, or even physiological, conditions is inherent in the chromosomes themselves. Oftentimes

they are not uniform in width; this is obviously so in *Ascaris*, and though less evident in other instances, this lack of uniformity has always to be reckoned with.

Our measurements were based partly on camera lucida drawings, which were made with special precautions to secure both accuracy and uniformity, and represented a constant magnification of 2520. They were checked by a well-adjusted screw micrometer eyepiece, though this could not be conveniently employed for any except the larger chromosomes owing to the relatively low magnifying power of the (No. 6 Zeiss) ocular as compared with the No. 18 oc. otherwise used.

Width Measurement of Chromosomes.

The widths of the chromosomes in microns, correct to the first place of decimals, are recorded on the graphs. The ordinates represent the number of counts made, the abscissæ the width, in microns, of the chromosomes. Each type of line illustrates the series of mitosis from which the measurements have been taken. The animals selected, with the exception of *Echinus esculentus*, are all included in Meek's first group of Metazoa, which according to his observations should have a uniform chromosome width of 0·83 μ.

The figures for the Plates have been drawn under the same magnification and under precisely identical conditions as regards the projections for measurement. Nuclei have been selected which show clearly the general character of the chromosomes, though perhaps only one or two of the latter may have been suitable for measurement. It will be realised that it was necessary to collect the measurements from a very large number of nuclei.

The width measurements recorded in the graphs represent :—

1. For somatic divisions: The width of the chromosome before it splits on the equatorial plate.

2. For the first meiotic (heterotype) division: The width of one of the two segments.

3. For the second meiotic (homotype) division: The width of the daughter-chromosome at early anaphase. Measurements of the width taken at earlier stages are untrustworthy owing to the indefinite shape of, and precocious fission in, the chromosomal thread.

PHYLUM VERTEBRATA.

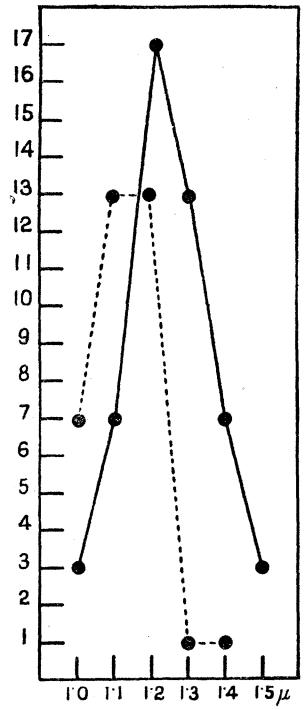
Triton cristatus (Plate 1, figs. 1 and 2).

Slides of Triton were used, made from excellent material lent by Miss Embleton. It had been fixed in Flemming's solution and stained with Heidenhain's hæmatoxylin.

Width measurements were taken from chromosomes of spermatogonial and secondary spermatocyte mitoses. Chromosomes of the spermatogonial divisions were

measured in late prophase, and as they were congregating on the spindle, no difficulty was experienced, as the chromosomes are large, homogeneous, and sharply defined. The width of the majority of the chromosomes was found to be 1·2 μ, but nearly as many had a width of 1·3 μ, and no chromosome narrower than 1 μ was observed.

The result of the measurement of secondary spermatocyte chromosomes shows the mean width to lie between 1·1 μ and 1·2 μ. MEEK, on the other hand, found the width to be invariably 0·83 μ.

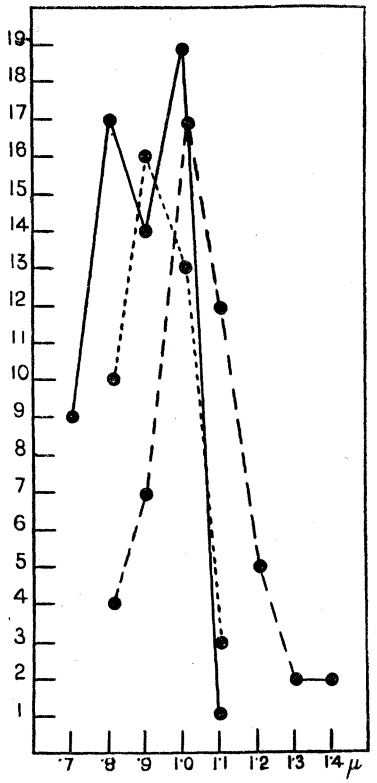


Triton cristatus.

Spermatogonial divisions.

Secondary spermatocyte divisions.

Measurements of univalent chromosome at the early anaphase of the heterotype division.



Gryllus domesticus.

Spermatogonial divisions.

Primary spermatocyte divisions.

Secondary spermatocyte divisions.

PHYLUM ARTHROPODA.

Gryllus domesticus (Plate 1, figs. 3, 4, and 5).

MEEK has measured the chromosomes of *Gryllus domesticus*, and finds the diameter to be invariably 0·83 μ, with the exception of the heterotropic chromosome, which has not been taken into consideration. Similarly, in our own investigation of *Gryllus domesticus*, the heterotropic chromosome has been ignored, though sometimes it could hardly be distinguished from the others.

The maximum number of measurements of the spermatogonial chromosomes

corresponds to a width of 1 μ, but, as there are almost as many measurements at 0·8 μ, with a slight drop in the numbers at 0·9 μ, it may be affirmed that the average width lies between 0·8 μ and 1 μ.

The primary spermatocyte chromosomes do not show a large variation, and their width works out at about 1 μ. The heterotropic chromosome is often most striking in the polar view of an equatorial plate (fig. 4).

A rest intervenes between the primary and secondary spermatocyte divisions, consequently they are easy of recognition.

The measurements of the secondary spermatocyte chromosomes show 0·9 μ as the most frequent width measurement result, with only a slight drop in the numbers of chromosomes having a width of 1 μ.

The results of the width measurements of the spermatogonial, primary, and secondary spermatocyte chromosomes give a comparatively slight range of variation.

Homarus gammarus (Plate 1, figs. 6, 7, 8, and 9).

The measurements of the chromosomes of *Homarus* and *Palæmon* were made from excellent slides prepared by Miss Ash, who kindly placed them at our disposal.

No spermatogonial divisions were found in Lobster, but primary and secondary spermatocyte divisions were present in abundance.

There are, apparently, two types of primary spermatocyte division figures: the one has smaller chromosomes, which are more or less tetrad-like bodies (figs. 6 and 7), whilst in the other they are obviously larger (figs. 8 and 9).

Figs. 6 and 7 have been drawn from a preparation fixed with Flemming solution, and figs. 8 and 9 from one fixed with acetic alcohol. At first it was thought that the appearance of the chromosomes might be due to the action of the fixative used. Subsequent research negatived this idea, as nuclei showing almost as marked differences as those figured were found on the same slide. It would involve detailed investigation to solve this problem. Both types of nuclei have been been measured, and the results combined and entered on the graph.

The measurement curve of the primary spermatocyte chromosomes shows a decided maximum for a width of 0·8 μ, with an almost equal number of variations from the mean on either side.

Considerable difficulty was encountered in measuring the secondary spermatocyte chromosomes, partly on account of their small size, and partly because primary spermatocyte divisions are constantly intercalated amongst the secondary spermatocyte divisions, making it almost impossible to discriminate between the two. The measurements entered on the graph have been taken exclusively from the small type of chromosome, and, in all probability, if a wider range of measurements had been made, the curve would have given higher width figures.

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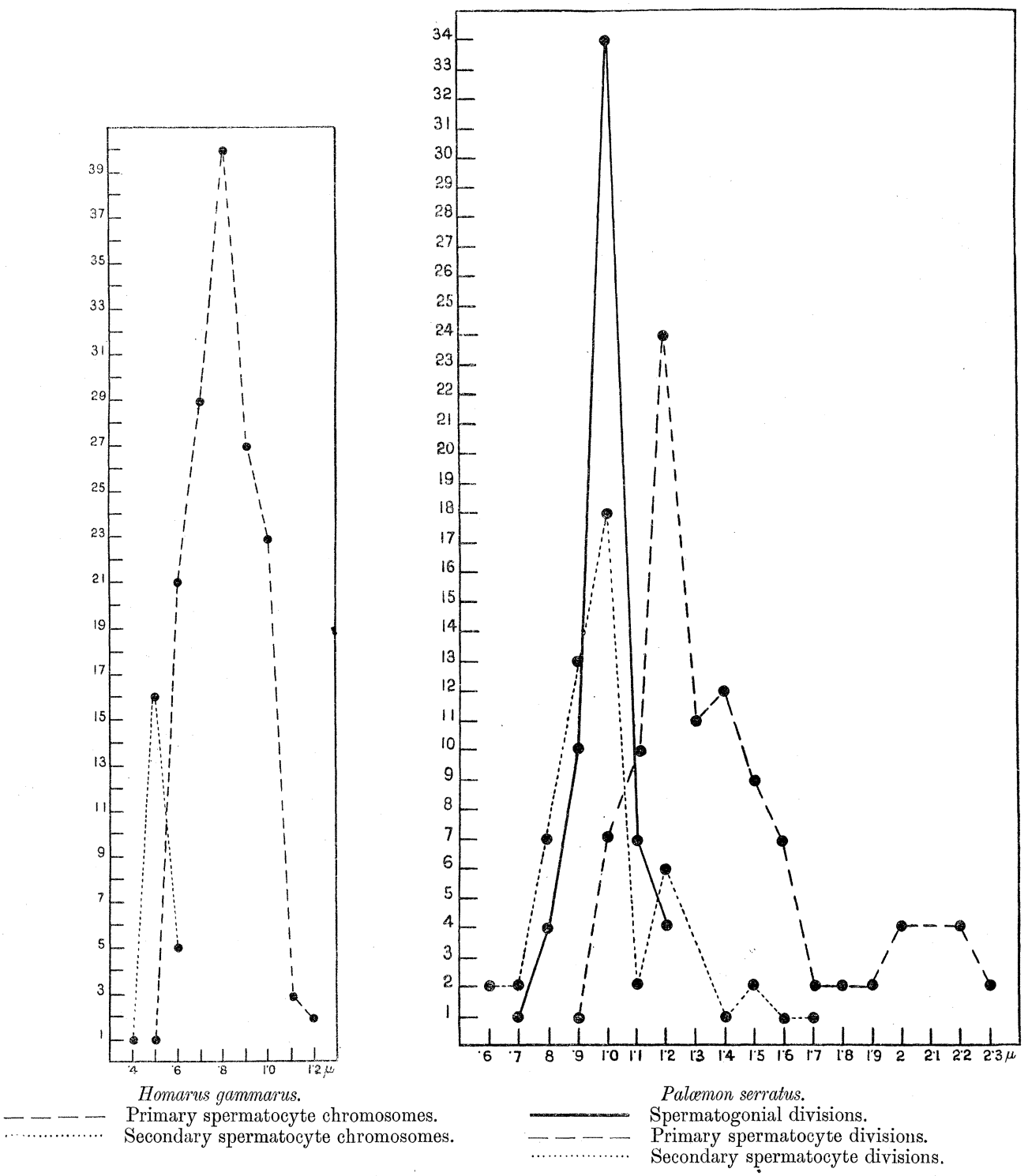


Palæmon serratus (Plate 1, figs. 10, 11, 12, 13, 14, and 15).

Although the Lobster and Prawn belong to the same section Macrura, yet their chromosomes are widely different in character and, what for our present purpose is specially important, in width.

In the spermatogonial divisions four chromosomes are strikingly larger than the rest (fig. 10), and the primary (figs. 11, 12, and 13) and secondary (fig. 15) spermatocyte divisions similarly contain two large chromosomes. These divide normally on the equatorial plates of both the heterotype (figs. 13 and 14) and homotype divisions, and have therefore been considered to be ordinary, and not heterotropic chromosomes. Consequently their width measurement has been taken and duly entered on the graph, by which their disparity in size is clearly brought out.

In the premeiotic spermatogonial divisions, in contrast to the above-mentioned meiotic divisions, the four large chromosomes are distinguished by their length and by their V shape (fig. 10). They closely resemble the heterotropic chromosomes of the somatic divisions of *Gryllus*. Their width is not appreciably greater than that of the ordinary, more rounded chromosomes. The majority of chromosomes have a width of 1 μ, with an approximately equal divergence on either side.

The polar view of the primary spermatocyte equatorial plate (fig. 11) shows the comparatively enormous size of the two chromosomes. These separate with the other bivalent chromosomes into their univalent halves (figs. 12 and 14) and one proceeds to either spindle pole. Drawings have been made of a polar view (fig. 12) and also of a profile view (fig. 13) of the chromosomes as they begin to move apart. Owing to the great difference in width between the smaller and the larger chromosomes, and to the variability of the latter, the curve of the width measurements extends over a wide range. It shows a decided maximum for a chromosome width of 1·2 μ, indicating the most frequent width of the smaller univalent chromosomes of the bivalent combination. The curve is then continued to 2·3 μ, the maximum width observed in the larger chromosomes.

The difference in chromosome size is maintained throughout the secondary spermatocyte divisions (fig. 15). The greatest number of width measurements gives 1 μ, but many values fall below that figure, whilst the large chromosomes may be as wide as 1·7 μ.

PHYLUM MOLLUSCA.

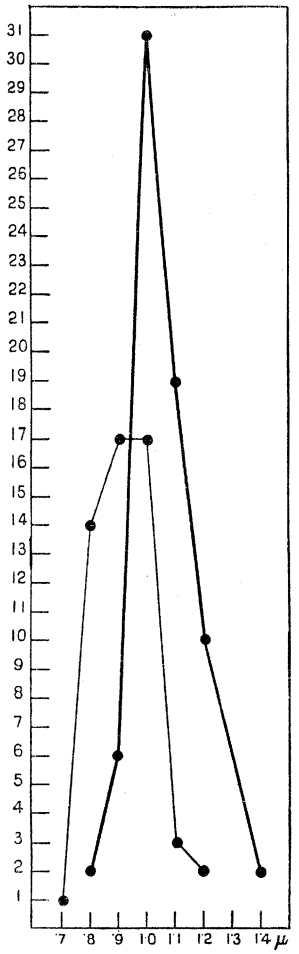
Helix pomatia (Plate 1, figs. 16, 17, and 18).

We possess a large number of slides of the hermaphrodite gland of *Helix pomatia*, which enabled us to study every phase of division. The measurements of the spermatogonial (fig. 16) and öogonial (fig. 17) chromosomes were alone recorded on the graph, as the striking gradations in size of the primary spermatocyte and oöcyte chromosomes (fig. 18) indicate that, for this animal at any rate, no sound conclusions can be founded on the assumption of uniformity in the width of the chromosomes.

It is, perhaps, not impossible that this great disparity in the size of the chromosomes may be related to the occurrence of dimorphic sperms in some nearly related molluscs.

The curve of the spermatogonial chromosomes has two apices, corresponding to widths of 0·9 μ and 1 μ respectively, with a far larger number of measurements below than above those figures.

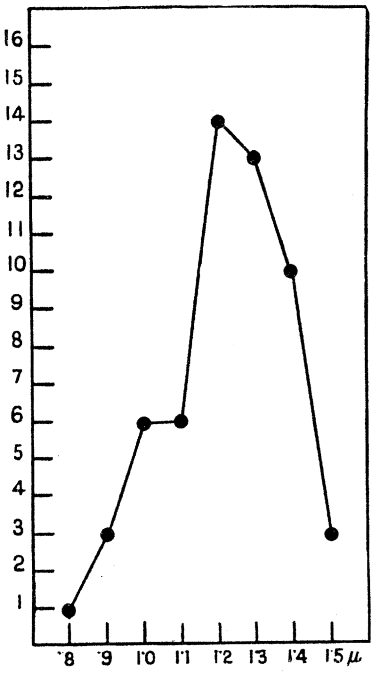
The majority of the oögonial chromosomes are 1 μ wide, with 30 measurements above that figure and only eight below. Therefore, although in both the spermatogonial and oögonial divisions the apex of the curves is at 1 μ, in the one case more width measurements have been recorded below, whilst in the other more width measurements have been recorded above that figure. The difference in width is apparent when the drawings of the two are compared (figs. 16 and 17). It is not surprising that the chromosomes associated with the formation of the egg should be larger than those connected with the sperm. Moreover, Conklin (1912) has shown that the chromosomes of the spermatid are usually smaller than are those of the oötid.



Helix pomatia.

Spermatogonial divisions.

Oögonial divisions.



Ascaris megalocephala ("*bivalens*").

First cleavage divisions.

PHYLUM NEMATHELMINTHIA.

Ascaris megalocephala, var. "*bivalens*" (Plate 1, figs. 19 and 20).

The chromosomes are somewhat club-shaped, with ends constantly wider than the intermediate parts (figs. 19 and 20). The straighter portions of the chromosomes were

alone measured. MEEK measured chromosomes from oögonial and primary oöcyte divisions and obtained a uniform result of 0·83 μ as the width of the chromosomes.

The measurements for our paper were taken from first segmentation divisions. The largest number of measurements (14) are recorded at 1·2 μ, but nearly as many (13) at 1·3 μ. Indeed, as the graph clearly shows, there is a good deal of variation in the widths of the chromosomes of this animal. This may be partly due to the fact that the chromosomes themselves are large, and hence the differences are more striking and more easily estimated. It is perhaps not necessary to say that in making the measurements we were alive to the difficulty which the form of the chromosomes imposed.

The result of measurements of a few of the higher animals (and we might easily have extended the list) suffices to show that the constancy of width attributed to the chromosomes within the range of the higher forms can hardly be admitted.

PHYLUM ECHINODERMATA.

Echinus esculentus (Plate 1, fig. 21).

Echinus esculentus is the only type that has been examined which comes under MEEK's second division of chromosome widths.

MEEK has measured the chromosomes of maturing ova and of the four-, eight-, and sixteen-cell stages of segmentation, and finds the width to be 0·42 μ (p. 38). Mr. DOBELL lent a slide of segmenting eggs, from which it was difficult, though possible, to make approximate chromosome measurements (fig. 21). The results showed 0·4 μ to be the most frequent width, with only a few measurements above that figure. This therefore agrees closely with MEEK's own results. But we cannot, in the light of the failure to establish anything like constancy amongst related genera in the higher animals, attach to this circumstance the same degree of importance which he has attributed to it.

PLANT KINGDOM.

PHANEROGAMIA.

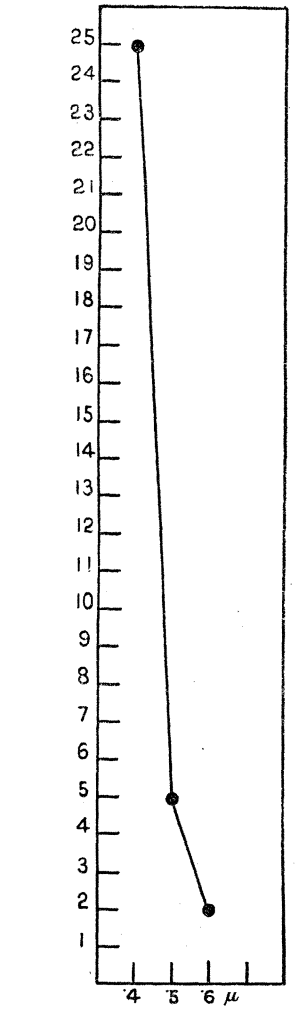
Family Compositæ.

Crepis virens (Plate 2, figs. 22, 23, 24, 25, and 26).

The chromosomes of *Crepis virens* are of an extremely viscous nature, which renders their outline so irregular that it is evident that their width measurement can neither be definite nor constant. Moreover in *C. taraxacifolia* this character is further accentuated so as to make it impossible in this species to gauge the average width of the chromosomes.

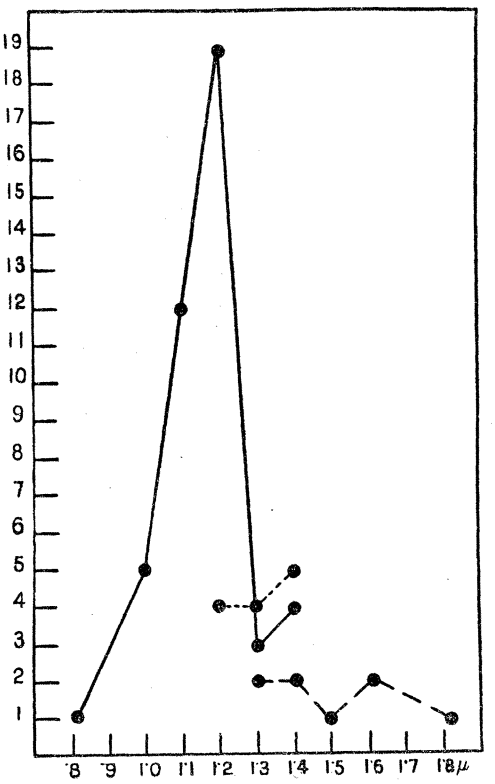
It has already been noted that the chromosomes of the archesporial divisions show a somewhat early split, and constantly become flattened prior to splitting (figs. 22

and 23). These facts add considerable complications to the taking of width measurements. In order to obviate error on this account only chromosomes in side view have been measured. The results give many widths of 1·2 μ, with some measurements at 1·1 μ.



Echinus esculentus.

——— Segmenting eggs.



Crepis virens.

——— Archesporial divisions.

— — — — Heterotype divisions.

..... Homotype divisions.

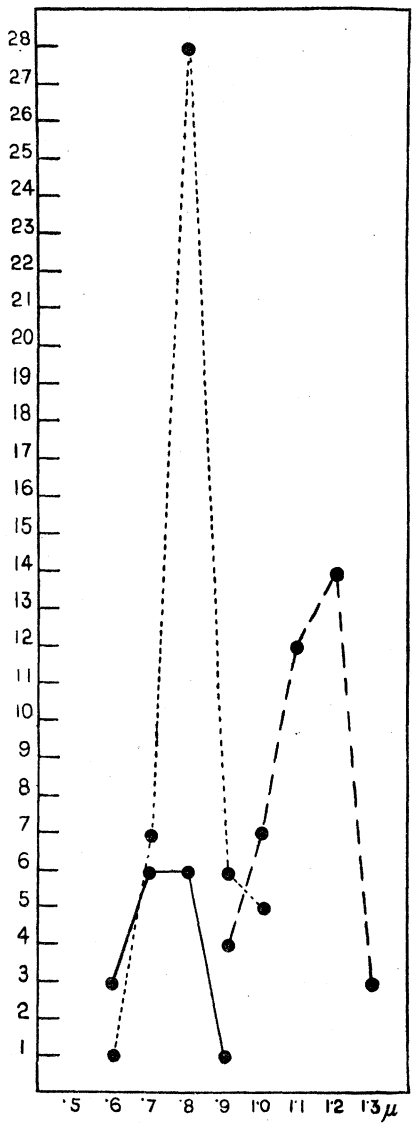
The heterotype chromosomes exhibit a wide range of elongation and contraction. After careful collection of the very few chromosomes that lent themselves to measurement (fig. 24) the results, when recorded, describe a most indefinite curve.

The same conditions were experienced with regard to the homotype divisions, and only very few measurable chromosomes could be found (fig. 26). These show a variation in width from 1·2 μ to 1·4 μ.

Family Primulaceæ.

Primula floribunda (Plate 2, figs. 27, 28, 29, 30 and 31).

In marked contrast to *Crepis*, *Primula* has sharply defined chromosomes. Moreover, they are approximately of the same size, and consequently the measurement curve shows comparatively little variation.



Primula floribunda.

——— Archesporial and somatic divisions.

— — — — Heterotype divisions.

..... Homotype divisions.

The measurements of the somatic chromosomes have not been taken exclusively from the archesporial nuclei, but also from the dividing tissue of the young stamen (figs. 27 and 28).

The maximum points of the curve correspond to widths of 0·7 μ and 0·8 μ. The heterotype chromosomes have been measured both in polar (fig. 29) and in profile (fig. 30) views of equatorial plates. Between 1·1 μ and 1·2 μ is the most uniform width of the univalent segment of the heterotype chromosome.

The width of the homotype chromosomes (fig. 31) is very constantly 0·8 μ, as may be clearly seen from the graph.

Family Liliaceæ.

Galtonia candicans (Plate 2, figs. 32, 33, 34, 35, 36, 37, 38, 39 and 40).

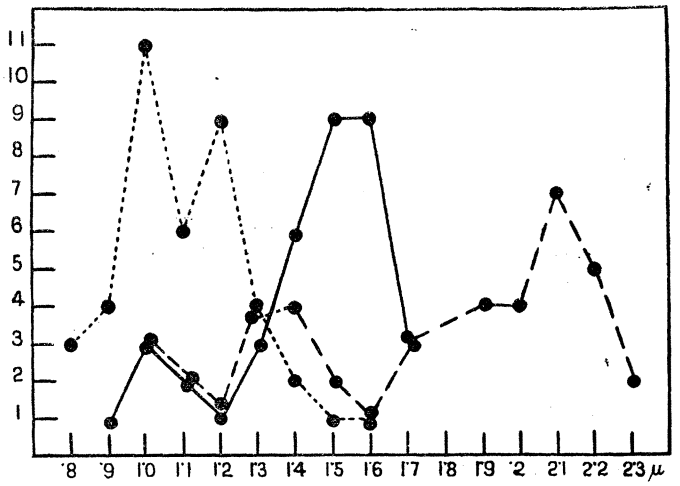
The curves of chromosome measurement are complicated in *Galtonia* owing to the unequal size, and also to the differences in width, of the chromosomes. In the archesporial divisions four of the chromosomes are decidedly smaller than the others, and the remaining 12 show considerable variation (fig. 30). Müller (1912) has clearly demonstrated this inequality in size in *Galtonia* (Taf. 1, figs. 35, 36 and 37) and in several other plants.

It will be seen from the graph that the width measurements of the small chromosomes have not been so frequently recorded as those of the larger chromosomes. This is due to the fact that they are in a minority in the nucleus, and hence do not afford so many chances for measurement.

The measurements of the archesporial chromosomes (fig. 33), when plotted out, lie on a curve with two apices, corresponding to 1 μ, the average width of the small

chromosomes, and to 1·5 μ and 1·6 μ, the most frequent widths of the larger chromosomes.

The extreme differences in size exhibited by the heterotype chromosomes is strikingly shown in the polar view of an equatorial plate (fig. 39). Such a figure indicates the irregular curve that will result from measurement records. The widths range from 1 μ to 2·3 μ, with more or less marked apices for widths of 1 μ, 1·3 μ and 1·4 μ, 1·9 μ and 2 μ, and 2·1 μ.



Galtonia candicans. ——— Archesporial divisions.
— — — — Heterotype divisions.
····· Homotype divisions.

Difficulty was experienced in obtaining measurable stages in the evolution of the homotype chromosomes. They are long and narrow before concentration, and when completely concentrated their outlines often become obliterated through close approximation. Consequently, it was found desirable to take some of the measurements from early anaphase (fig. 40). Again, the results describe a most irregular curve. The measurements of 0·8 μ and 0·9 μ represent the widths of the small chromosomes; the intermediate chromosomes are 1 μ and 1·2 μ wide, as shown by the large number of measurements obtained at those figures; while, as may be seen from the curve, there are a few measurements of larger chromosomes, the greatest width observed being 1·6 μ.

Cryptogamia.

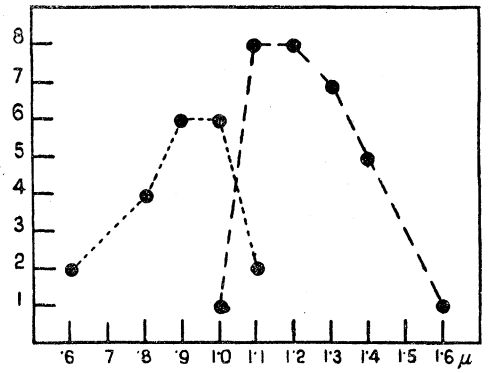
FILICINÆ.

Family Polypodiaceæ.

Polypodium aureum (Plate 2, figs. 41, 42 and 43).

The slides with archesporial divisions were not sufficiently clear to allow of accurate chromosome measurement, and they are therefore omitted from the annexed graph.

Fig. 41 is a typical example of the polar view of a heterotype equatorial plate, and in some isolated chromosomes (fig. 42) the breadth was easy to ascertain. The results show the greater number of measurements to be at 1·1 μ and 1·2 μ, with only one less



Polypodium aureum. — — — — Heterotype divisions.
..... Homotype divisions.

at 1·3 μ, so that it may be affirmed that the average width of the heterotype chromosomes lies between 1·1 μ and 1·3 μ.

The width measurements of the homotype chromosomes are almost all 0·9 μ and 1 μ.

Family Osmundaceæ.

Osmunda regalis (Plate 2, figs. 44 and 45).

It was found to be impossible to measure the heterotype chromosomes of *Osmunda regalis*, as they tend to mass together, and consequently the limits of their individual outlines are obscured.

There is little variation in the widths of either the archesporial (fig. 44) or homotype (fig. 45) chromosomes. Those of the archesporium are easy to measure, for they are still homogeneous and unsplit as they arrange themselves on the equatorial plate.

It will be seen from the graph that in both cases the maximum point of the curve corresponds to a width of 0·8 μ, but whilst in the archesporial divisions this figure represents a more or less constant width, in the homotype divisions there are approximately as many measurements at 0·9 μ, signifying that the width lies between 0·8 μ and 0·9 μ.

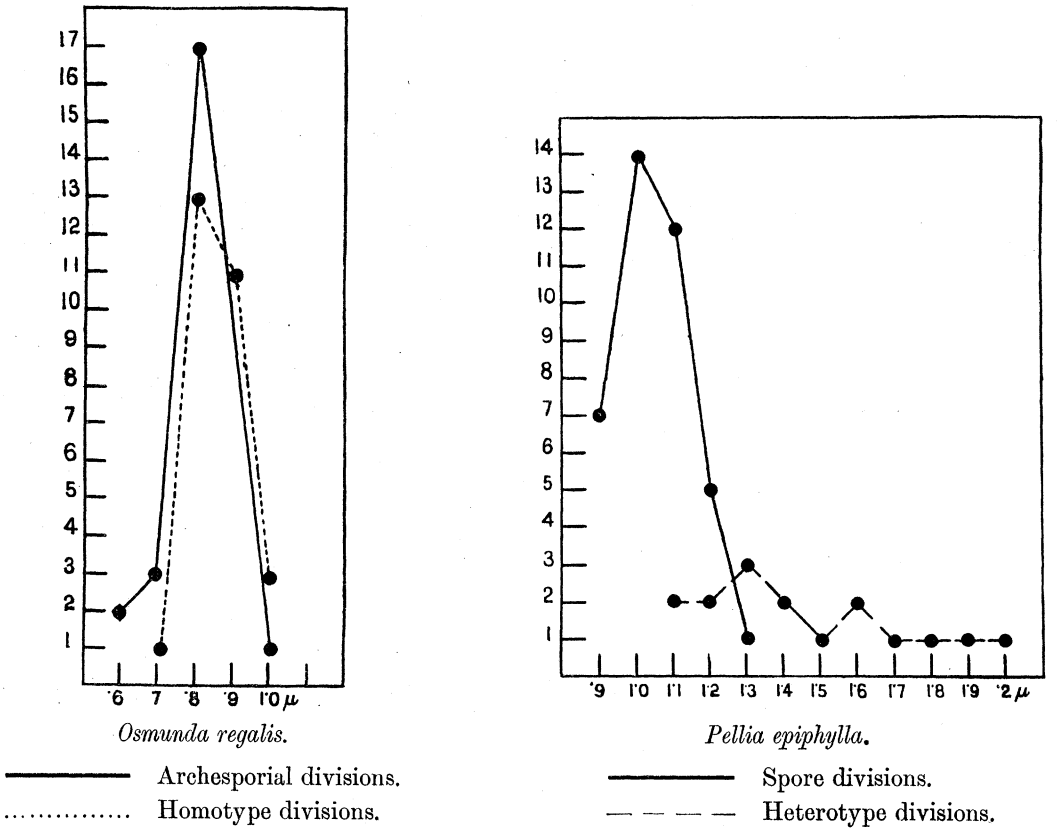
HEPATICÆ.

Pellia epiphylla (Plate 2, figs. 46 and 47).

The width measurements of the somatic chromosomes have been taken from spore divisions (fig. 46). These chromosomes, owing to their sharp definition, lent themselves admirably to measurement. The maximum number of measurements

correspond to the width of 1 μ, with more measurements above than below that figure.

The widths of the heterotype chromosomes (fig. 47) give a wide variation, and the chief conclusion to be drawn from the measurement recorded on the graph is that the width of the chromosomes is a variable character of this plant.



Osmunda regalis.

Archesporial divisions.
Homotype divisions.

Pellia epiphylla.

Spore divisions.
Heterotype divisions.

Summary.

1. The number of the chromosomes in nearly related species affords no certain indication of the value of the K/P relation.

2. The total amount of chromosome substance in the nuclei of each of the two types of hybrids known as *Primula Kewensis* is the same. The nuclei of the one form of hybrid contain twice as many chromosomes as the nuclei of the other type, but the increase in number is associated with a corresponding diminution in size.

3. No animal or plant examined has been found to have a constant chromosome width. The ordinary extent of the variation is comparable with that found in other structures, whether of animals or plants.

4. The width of a chromosome is seldom uniform throughout its length.

5. The nuclei of some animals and plants possess chromosomes of very different sizes; and, consequently, the width measurements vary within wide limits.

6. The chromosomes in oögonial divisions may be larger and wider than those in corresponding spermatogonial divisions.

7. Chromosome width cannot be intimately correlated with phylogenetic order, for closely related forms may possess chromosomes differing widely in shape and size and character.

The graphs illustrate two points, (1) that in every animal and plant examined the width of the chromosomes was found to be inconstant and to exhibit more or less variation; (2) that chromosome width cannot be strictly correlated with the order of phylogeny. It is true that many of the more lowly animals and plants have smaller and narrower chromosomes, as compared to those of higher forms. But the example of the Prawn and Lobster, described above, suffices to prove conclusively that phylogenetic affinity is not, necessarily, correlated with similarity in chromosome width.

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EXPLANATION OF PLATES.

All the figures were drawn with a large camera lucida under a 2 mm. apochr. hom. imm., Zeiss, N.A. 1·40, with comp. oc. 18. ×2520.

Plate 1.

Fig. 1.—*Triton cristatus.* Spermatogonial prophase. Chromosomes about to go on to the spindle.

Fig. 2.—Polar view of an equatorial plate of a secondary spermatocyte division.

Fig. 3.—*Gryllus domesticus.* Prophase of a spermatogonial division. One of the heterotropic chromosomes is to be seen.

Fig. 4.—Polar view of an equatorial plate of a primary spermatocyte division. Note the relatively large size of the heterotropic chromosome.

Fig. 5.—Polar view of an equatorial plate of a secondary spermatocyte division.

Fig. 6.—*Homarus gammarus.* Polar view of an equatorial plate of a primary spermatocyte division, showing the smaller type of chromosome.

Fig. 7.—Profile view of the same, showing a few of the smaller type of chromosomes.

Fig. 8.—Polar view of an equatorial plate of a primary spermatocyte division, showing the larger type of chromosomes.

Fig. 9.—Profile view of the same, showing three of the larger type of chromosomes.

Fig. 10.—*Palæmon serratus.* Polar view of an equatorial plate of a spermatogonial division. Note the four long V-shaped chromosomes.

Fig. 11.—Polar view of an equatorial plate of a primary spermatocyte division. Note the two very large chromosomes.

Fig. 12.—Polar view of an equatorial plate of a primary spermatocyte division. The chromosomes are just separating.

Fig. 13.—Profile view of an equatorial plate of a primary spermatocyte division.

Fig. 14.—Two large chromosomes, showing their method of division on the heterotype equatorial plate.

Fig. 15.—Polar view of an equatorial plate of a secondary spermatocyte division. Note the two large chromosomes.

Fig. 16.—*Helix pomatia.* Prophase of a spermatogonial division.

Fig. 17.—Prophase of an oögonial division.

Fig. 18.—Diakinesis of a primary oöcyte division. Note the extreme variations in size of the chromosomes.

Fig. 19.—*Ascaris megalocephala*, var. "*bivalens.*" Polar view of an equatorial plate of a first segmentation division.

Fig. 20.—The same.

Fig. 21.—*Echinus esculentus.* Spindle figure of a segmenting egg.

Plate 2.

Fig. 22.—*Crepis virens.* Archesporium. Polar view of an equatorial plate. The chromosomes show various stages in the process of splitting into the two daughter chromosomes.

Fig. 23.—The splitting of the chromosomes is farther advanced than in the previous figure.

Fig. 24.—Pollen mother-cell. Polar view of an equatorial plate of the heterotype division.

Fig. 25.—Pollen mother-cell. Telophase of the heterotype division. In the upper nucleus the resolution of the three chromosomes into paired rows of granules is to be seen, while in the lower nucleus the individuality of the three chromosomes is already becoming lost to view owing to the dispersal of the granules.

Fig. 26.—Polar view of an equatorial plate of the homotype division.

Fig. 27.—*Primula floribunda.* Prophase taken from the tissue of a stamen.

Fig. 28.—The same.

Fig. 29.—Pollen mother-cell. Polar view of an equatorial plate of the heterotype division.

Fig. 30.—Section of a profile view of the same.

Fig. 31.—Polar view of an equatorial plate of the homotype division.

Fig. 32.—*Galtonia candicans.* Root. Approximation in pairs of linin strands bearing chromatin, which subsequently condense to form the chromosomes.

Fig. 33.—Archesporium. Polar view of an equatorial plate.

Fig. 34.—Root. Section of an equatorial plate. The chromosomes show longitudinal fission throughout their length. Figs. 34–37 illustrate the progressive stages in the concentration of the daughter chromosomes as they separate from one another and pass to the spindle poles.

Fig. 35.—Root. The daughter chromosomes are beginning to separate on the equatorial plate.


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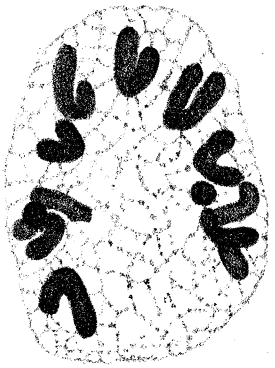
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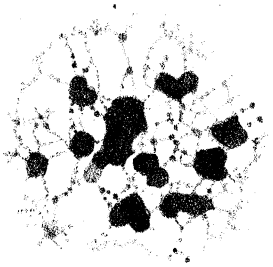
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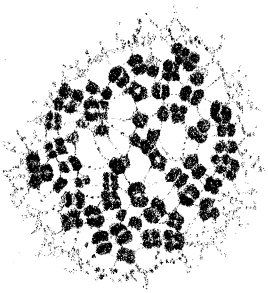
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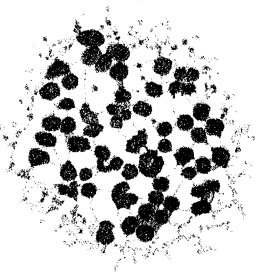
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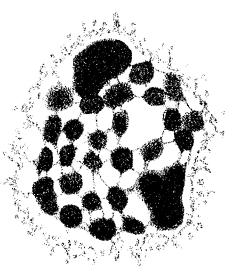
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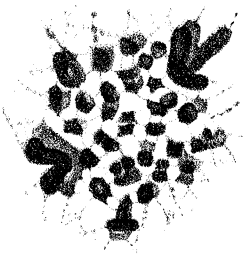
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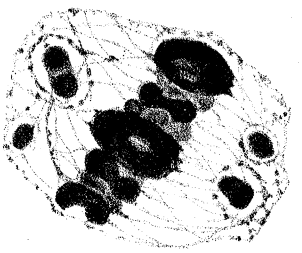
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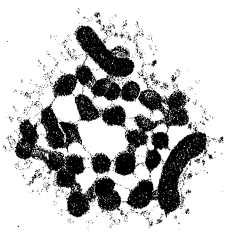
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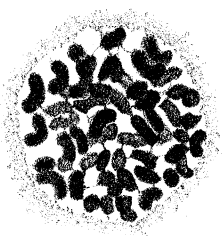
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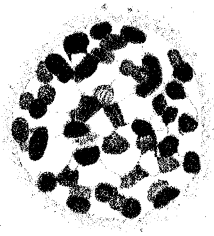
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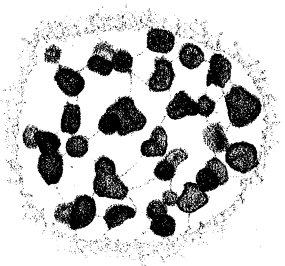
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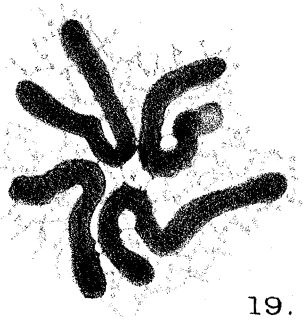
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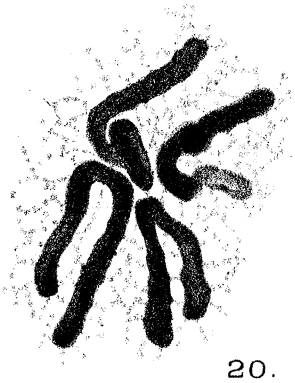
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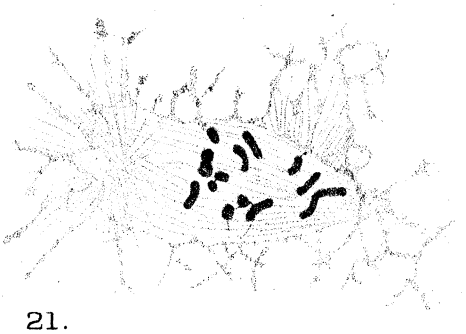
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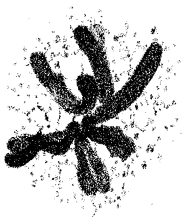
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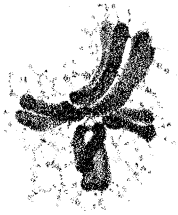
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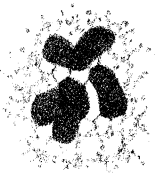
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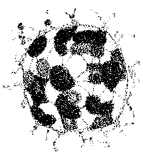
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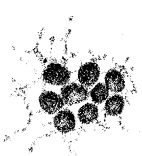
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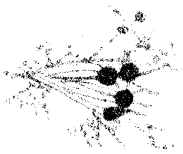
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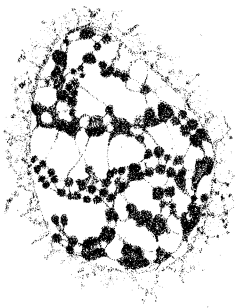
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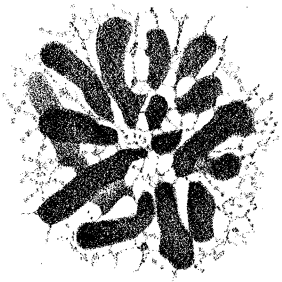
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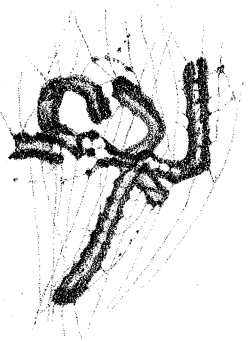
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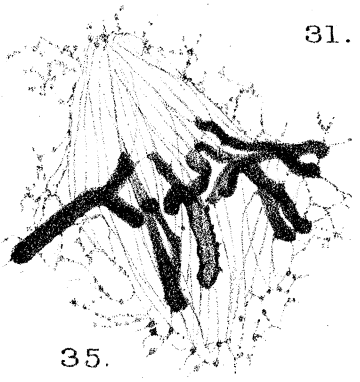
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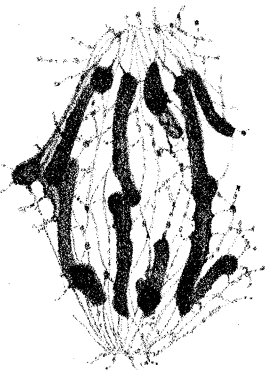
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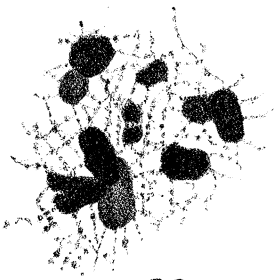
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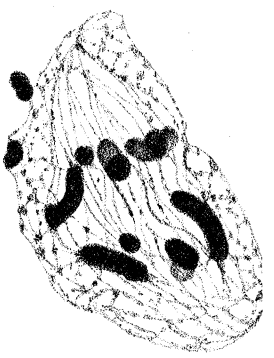
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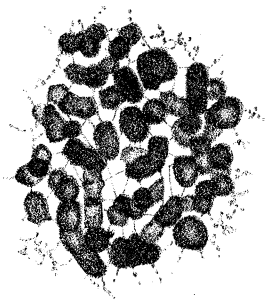
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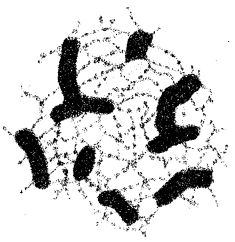
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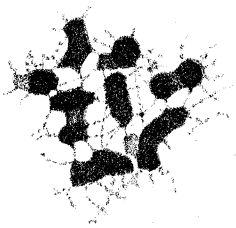
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Fig. 36.—Root. The large daughter chromosomes are proceeding to the spindle poles, but are still joined at one end. The small chromosomes have already arrived at the poles.

Fig. 37.—Root. Anaphase. The daughter chromosomes have completely separated.

Fig. 38.—Pollen mother-cell. The bivalent chromosomes are splitting into their univalent segments after the second contraction. Note the irregular outline of the newly split portions previous to concentration.

Fig. 39.—Pollen mother-cell. Polar view of an equatorial plate of the heterotype division.

Fig. 40.—Anaphase of the homotype division.

Fig. 41.—*Polypodium aureum*. Spore mother-cell. Polar view of an equatorial plate of the heterotype division.

Fig. 42.—Three isolated chromosomes taken from the same stage as fig. 41.

Fig. 43.—Section of a prophase of the homotype division.

Fig. 44.—*Osmunda regalis*. Archesporial division. A sectional view of some of the chromosomes arranging themselves on the equatorial division.

Fig. 45.—Anaphase of the homotype division.

Fig. 46.—*Pellia epiphylla*. Spore division. Chromosomes going on to the spindle.

Fig. 47.—Polar view of an equatorial plate of the heterotype division.

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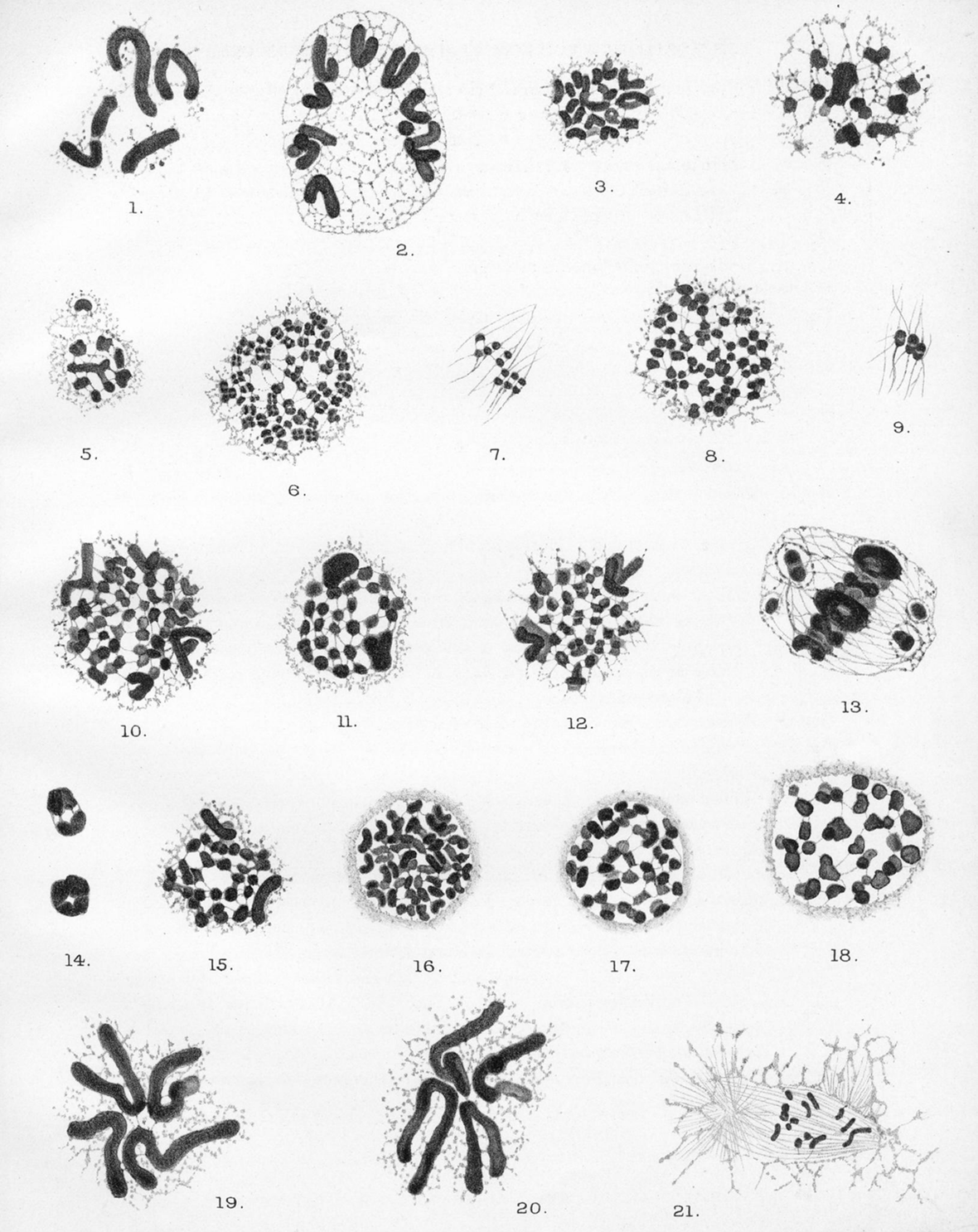

PLATE 1.

Fig. 1.—*Triton cristatus.* Spermatogonial prophase. Chromosomes about to go on to the spindle.

Fig. 2.—Polar view of an equatorial plate of a secondary spermatocyte division.

Fig. 3.—*Gryllus domesticus.* Prophase of a spermatogonial division. One of the heterotropic chromosomes is to be seen.

Fig. 4.—Polar view of an equatorial plate of a primary spermatocyte division. Note the relatively large size of the heterotropic chromosome.

Fig. 5.—Polar view of an equatorial plate of a secondary spermatocyte division.

Fig. 6.—*Homarus gammarus.* Polar view of an equatorial plate of a primary spermatocyte division, showing the smaller type of chromosome.

Fig. 7.—Profile view of the same, showing a few of the smaller type of chromosomes.

Fig. 8.—Polar view of an equatorial plate of a primary spermatocyte division, showing the larger type of chromosomes.

Fig. 9.—Profile view of the same, showing three of the larger type of chromosomes.

Fig. 10.—*Palæmon serratus.* Polar view of an equatorial plate of a spermatogonial division. Note the four long V-shaped chromosomes.

Fig. 11.—Polar view of an equatorial plate of a primary spermatocyte division. Note the two very large chromosomes.

Fig. 12.—Polar view of an equatorial plate of a primary spermatocyte division. The chromosomes are just separating.

Fig. 13.—Profile view of an equatorial plate of a primary spermatocyte division.

Fig. 14.—Two large chromosomes, showing their method of division on the heterotype equatorial plate.

Fig. 15.—Polar view of an equatorial plate of a secondary spermatocyte division. Note the two large chromosomes.

Fig. 16.—*Helix pomatia.* Prophase of a spermatogonial division.

Fig. 17.—Prophase of an oögonial division.

Fig. 18.—Diakinesis of a primary oöcyte division. Note the extreme variations in size of the chromosomes.

Fig. 19.—*Ascaris megalocephala,* var. "*bivalens.*" Polar view of an equatorial plate of a first segmentation division.

Fig. 20.—The same.

Fig. 21.—*Echinus esculentus.* Spindle figure of a segmenting egg.

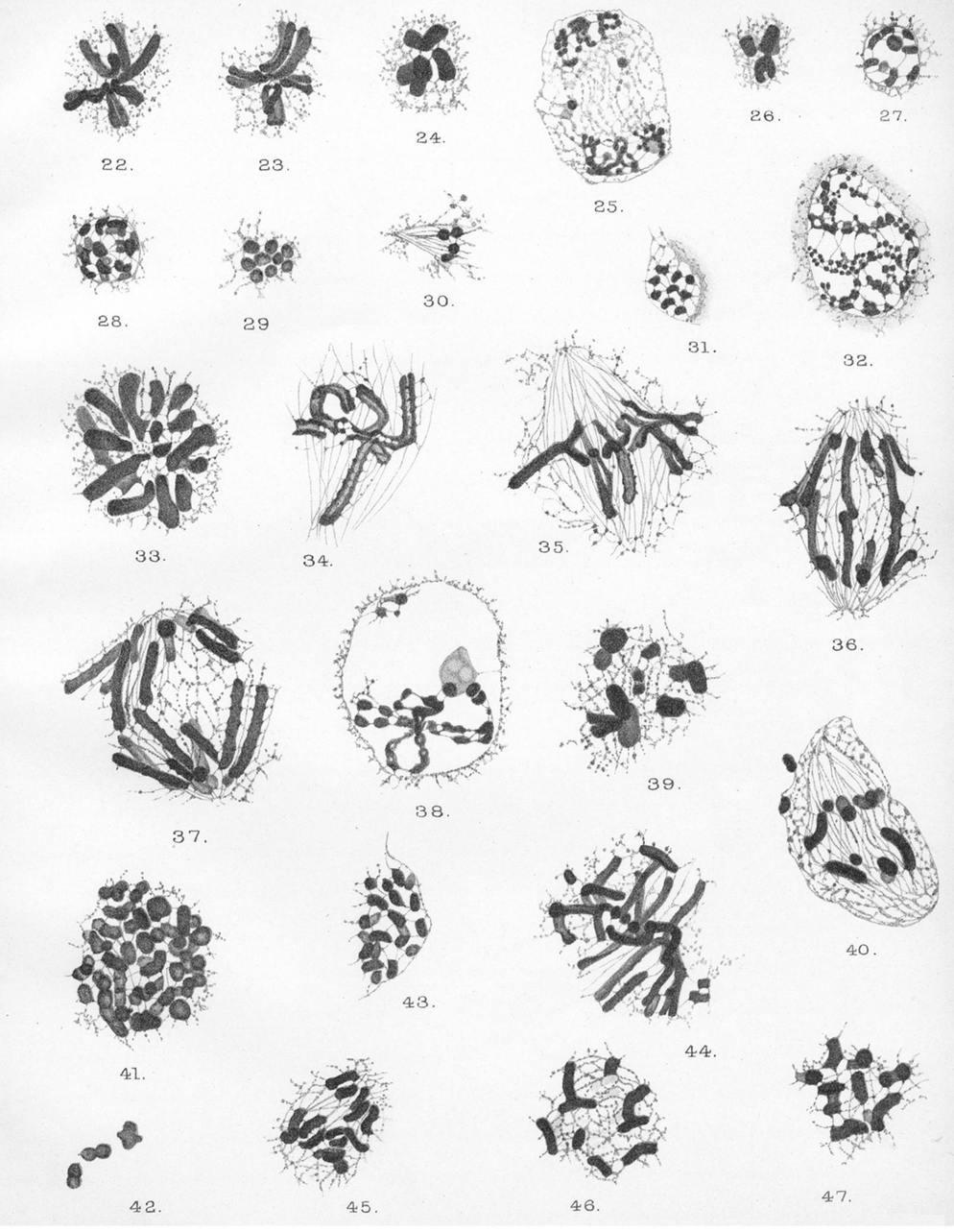

Plate 2.

Fig. 22.—*Crepis virens.* Archesporium. Polar view of an equatorial plate. The chromosomes show various stages in the process of splitting into the two daughter chromosomes.

Fig. 23.—The splitting of the chromosomes is farther advanced than in the previous figure.

Fig. 24.—Pollen mother-cell. Polar view of an equatorial plate of the heterotype division.

Fig. 25.—Pollen mother-cell. Telophase of the heterotype division. In the upper nucleus the resolution of the three chromosomes into paired rows of granules is to be seen, while in the lower nucleus the individuality of the three chromosomes is already becoming lost to view owing to the dispersal of the granules.

Fig. 26.—Polar view of an equatorial plate of the homotype division.

Fig. 27.—*Primula floribunda.* Prophase taken from the tissue of a stamen.

Fig. 28.—The same.

Fig. 29.—Pollen mother-cell. Polar view of an equatorial plate of the heterotype division.

Fig. 30.—Section of a profile view of the same.

Fig. 31.—Polar view of an equatorial plate of the homotype division.

Fig. 32.—*Galtonia candicans.* Root. Approximation in pairs of linin strands bearing chromatin, which subsequently condense to form the chromosomes.

Fig. 33.—Archesporium. Polar view of an equatorial plate.

Fig. 34.—Root. Section of an equatorial plate. The chromosomes show longitudinal fission throughout their length. Figs. 34–37 illustrate the progressive stages in the concentration of the daughter chromosomes as they separate from one another and pass to the spindle poles.

Fig. 35.—Root. The daughter chromosomes are beginning to separate on the equatorial plate.

Fig. 36.—Root. The large daughter chromosomes are proceeding to the spindle poles, but are still joined at one end. The small chromosomes have already arrived at the poles.

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