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The Aloinae: A Cytological Study, with Especial Reference to the Form and Size of the Chromosomes

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V. *The Aloinæ: a Cytological Study, with Especial Reference to the Form and Size of the Chromosomes.**

By Nesta Ferguson.

Communicated by Sir John B. Farmer, *F.R.S.*

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(Plates 18, 19.)

Contents.

I.—Introduction.

The original object of this research was to make as wide a survey as possible of the numbers, form and size of the chromosomes in the members of the Liliaceæ. In the present contribution, the results are recorded from a small division only of this large natural order. The sub-division, *Aloinæ*, attracted attention early in the investigation; the more especially since at the beginning of this research, with the exception of a brief description by Clemens Müller (18) of a somatic metaphase of a species of *Aloë* no cytological details of the group were available. While this research was in progress several papers have appeared in America (Taylor (30), (31), (32), (33)) which deal with the form and construction of chromosomes in several species of this group. These results will be discussed in a succeeding section.

Systematic Position and General Characteristics of the Aloinæ.

According to the classification in Engler and Prantl's *Pflanzenfamilien* (6), one of the tribes of the Natural Order Liliaceæ is given as the *Asphodeloideæ*. This tribe is

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further divided, and among the divisions is that of the *Aloineæ*, which is again sub-divided into two associations of genera :—

(1) *Kniphofinæ*, including *Kniphofia* and *Notosceptrum*.

(2) *Aloinæ*, including *Aloë*, *Gasteria*, *Apicra*, *Haworthia*, and *Lomatophyllum*.

Results obtained from a cytological comparison of a number of species from the four genera *Aloë*, *Gasteria*, *Haworthia* and *Apicra* are here described. No material from the genus *Lomatophyllum* was available, and I am given to understand that hitherto this genus has not flowered in England.

The plants belonging to the *Asphodeloideæ-Aloineæ-Aloinæ* are all typical Xerophytes characterised by thick fleshy leaves, the majority of the species growing on the dry steppes of the South African Karroo,* which bounds the south-west region of the Cape of Good Hope on the whole of the north and north-east sides.

The greatest range in vegetative structure occurs in the genus *Aloë*, species of which give examples of short-stemmed and long-stemmed forms, either branched or unbranched, forming all gradations in shrub and tree formation. One of the largest is *Aloë dichotoma*, so frequently described by travellers in Namaqualand as one of the characteristic features of that country. The plants reach a height of 20–30 feet with a trunk 3–4 feet in diameter near the base. This is surpassed in size only by *Aloë Bainesii*, whose branched stem is often 40–60 feet high with a trunk 4–5 feet in diameter (1). This species is a native of Natal and of the eastern coastal region of the province of the Cape of Good Hope, in the district geographically known as Kaffraria. At the other extreme are a number of species with rosettes of leaves borne at the surface of the ground, *e.g.*, *Aloë humilis*.

Some species of *Gasteria* and *Haworthia* have a half-shrubby habit, but more frequently the members of these two genera, like *Apicra*, are herbaceous plants, with their leaves forming loose or compact rosettes, or, in *Gasteria*, arranged in two series.

The flowers are borne on a racemose inflorescence, which may be single or branched. The perianth is gamophyllous ; forming a straight or curved tube in *Aloë*, *Gasteria* and *Apicra*, but bilabial in *Haworthia*, each lip consisting of three segments.

The number of species given by the systematists varies, and there is some lack of uniformity in the nomenclature. Baker (1) describes 86 species of *Aloë*, 45 of *Gasteria*, 59 of *Haworthia* and 7 of *Apicra*, while Engler's (6) classification deals with almost the same numbers, although only about 35 species of *Gasteria* are recognised. Schönland (28) more recently gives the numbers of species as about 120 for *Aloë*, 50 for *Gasteria*, 62 for *Haworthia*, and 8 for *Apicra*. New species, notably of *Aloë*, have been added to this list during recent years by naturalists in South Africa. (20 (1) (2) (3) etc.)

The systematists base the sub-division of the *Aloinæ* on the nature and method of

* Karroo, " a badly defined geographical term, meaning the interior part of the Cape Province, in which the vegetation consists largely of dwarf shrublets." (Schönland, 1924 (29), p. 459.)

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dehiscence of the fruit, the manner of dehiscence of the anthers, and the vegetative habit. (RENDLE (22).)

II.—MATERIAL AND METHODS.

The material for this research was mainly obtained from the collection of succulent plants in the Royal Botanic Gardens at Kew, and I wish to take this opportunity of thanking the Director for granting permission to use this material. I wish also here to acknowledge gratefully the courtesy and helpfulness of Mr. T. W. TAYLOR, of the Tropical Department of the Royal Botanic Gardens at Kew.

A group of species of *Gasteria* and *Haworthia* was obtained from the interesting collection of plants belonging to W. HORTON, Esq., of Liverpool, to whom my thanks are cordially given.

The usual cytological fixatives were used. Considerable difficulty was experienced with certain species, and many collections unfortunately were not useful for the purpose of this investigation. This was due to the fact that, while anthers in certain stages appeared to have undergone the various processes of preparation with good results, others with identical treatment, particularly with the pollen mother cells in later stages from diakinesis in the heterotype division onwards, were unsatisfactory; the chromatin was often clumped and the nuclear contents stained in a hard uniform manner in which all detail was obscured. Examination showed that the mother cell wall is usually considerably thickened at these stages. Possibly this hampers the penetration of the fixative with the result that the fixation is poor. A further difficulty which has limited the number of species for which results have been obtained is due to the fact that the sporogenous tissue is sometimes abortive, and in the young flower-buds this is only brought to light after sectioning.

On the whole, standard and medium strengths of chromacetic gave the most uniformly good results; ALLEN'S modification of BOUIN'S fixative gave excellent results for some species but was worthless for others.

Since the idea of the research was to cover a wide range of plants in this Natural Order, it was obviously not possible to compare in all species the effects of the use of different fixatives. In one or two instances several fixatives were employed for comparative purposes. In only few instances was this procedure possible, since in some species very few flowers are borne on the inflorescence and the time and frequency of flowering is irregular in cultivation.

In order to obtain results as nearly reliable as possible for comparative work, the actual measurements of the chromosomes (Section V) were made on material fixed in the same fixative, and standard chromacetic giving very fair fixation was chosen, as the results in this were more uniform. Unless otherwise stated in Section V, the flower-buds from which the measurements are taken were all fixed in this strength of chromacetic acid.

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The flower-buds were picked from the plants and either directly immersed in the fluid or first dipped into slightly warmed alcohol (usually 30 per cent.) (*cp.* DIGBY 5). The outer perianth was stripped off to expose the stamens and gynœcium and so provide for as rapid penetration of the fixing fluid as possible. For all the water fixatives used it was found necessary to use the exhaust pump to facilitate penetration.

After fixation and washing the material was gradually dehydrated and embedded in paraffin wax, clearing with cedar oil or xylol. Microtomed sections (10 μ or 12 μ thick) were stained with HEIDENHAIN'S Iron Hæmatoxylin with or without counterstain, or, for certain stages, with DELAFIELD'S Hæmatoxylin.

Sixteen species of *Aloë*, eighteen species of *Gasteria*, sixteen species of *Haworthia*, and four species of *Apicra* have been examined in this group.

III.—CHROMOSOME SHAPE.

The occurrence of chromosomes of a characteristic and sometimes specialised form is not uncommon in plant nuclei. Among other features the occurrence of constrictions appears to be widespread, and since FRASER and SNELL (9) described their occurrence in the chromosomes of *Vicia Faba* constrictions have been observed in the chromosomes of the nuclei of a large number of plant species.

The position of these constrictions may be subterminal. Such constrictions were found by NEWTON (19) to occur in all the chromosomes during the somatic divisions in *Galtonia*. The position of the constriction in that genus is associated with the attachment of the spindle fibres, but NEWTON shows that they are definite features of the chromosome, since they could be seen in prophase stages and were not, therefore, the result of mechanical forces acting during the division stages.

On the other hand, the constrictions may occur in a position quite independently of the point of attachment of the spindle fibre. This is the condition in *Vicia Faba* and other species of *Vicia*, in which genus SAKAMURA ((25) and (26)) claims that the position of the constriction in the chromosomes makes it possible to distinguish one species from another by cytological inspection. In *Tulipa* a similar claim is made by NEWTON.

Observations in the Aloinæ.

1. *Somatic Divisions.*—An inspection of the drawings reproduced in Plates 18 and 19 shows that throughout the sub-division *Aloinæ* of the Liliaceæ there are constrictions, usually in a sub-terminal position, in the lengths of the chromosomes. The occurrence of these constrictions is more easily demonstrated at certain stages than at others. For example, in the somatic divisions (Plate 18, figs. 1–9) the evidence is clear. Fig. 9 is a somatic prophase from *Apicra deltoidea*, and in this there is a distinct separation between the constricted parts of the somatic chromosome. As condensation of the chromosome proceeds the separated parts must draw together again, since the amount of separation of the constricted portion at metaphase is never so great as that shown in the prophase

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figured. Figs. 1–4 are nuclei of various species of *Aloë*; figs. 1 and 2 are somatic metaphases in flower-buds, while Fig. 3 is part of a tapetal nucleus showing the constriction in some of the chromosomes. Fig. 4 is drawn from a neighbouring tapetal nucleus in anaphase, two chromosomes of which are selected to show the main constriction and a secondary constriction at the ends of the chromosomes away from the pole.

In figs. 5 and 6 the position of the constriction in *Gasteria* is seen to be associated with the attachment of the spindle fibres to the chromosomes, and the position of the constriction in one pair of long chromosomes is seen in fig. 6 to be farther removed from the end of these chromosomes. The length of the constricted portion in these two chromosomes is two to three times the length of the constricted portion of the other chromosomes in the chromosome groups. Fig. 7 is a metaphase of *Haworthia hybrida* with fourteen somatic chromosomes. The constricted ends can be clearly seen only in three or four of the longer chromosomes of this group, the orientation of the other chromosomes not being favourable for their observation. Fig. 8 shows the constrictions in a dividing nucleus of *Haworthia tesselata parva*, a tetraploid species with twenty-eight chromosomes in its somatic nuclei.

In all the metaphase figures the general rule appears to be that the end bearing the constriction is towards the centre of the plate, and it is evident from the nuclei at anaphase that it is near this end that the spindle fibres are attached. This is, at any rate, the point of the chromosomes which leads in the journey to the poles of the spindle.

2. *Meiotic Divisions.*—The most unfavourable stage for demonstrating the presence of constrictions appears to be the heterotypic metaphase in polar view. At metaphase the chromosomes reach their maximum condensation and the constriction can rarely be observed. In one or two species, notably *Aloë arborescens Natalensis*, where the constrictions are, at other stages, very well marked, it is possible to see the suggestion of this constriction even at the heterotypic metaphase in some of the univalent halves of the bivalent chromosomes (fig. 14).

Occasionally a chromosome in the nuclei of other species at metaphase suggests the presence of a constriction; at earlier and at later stages it can be seen that constrictions are constant features not only of somatic chromosomes, but also of the chromosomes during meiosis. In profile view of the heterotypic spindles (Plate 19, figs. 21–23), the only evidence during metaphase and early anaphase of this differentiation is given by the fact that the spindle fibre is not exactly terminal in the large chromosomes, and in figs. 22 and 23 of *Gasteria nigricans platyphylla* the very marked bend in each univalent of one bivalent is a feature of all the nuclei observed.

At diakinesis the constricted parts are sometimes clearly demonstrated (figs. 10, 11, 12), although frequently in other nuclei which are apparently well fixed all evidence of the constriction may be lost. Possibly these are later stages of condensation of the chromosomes, or possibly, as TAYLOR suggests, the chromosome does condense longitudinally during fixation if the penetration of the fixative is slow.

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Fig. 10 shows the occurrence of more than one constriction in one condensing pair of chromosomes in a nucleus of *Aloë Abyssinica*, while in a second bivalent, satellites of small magnitude occur in addition to the usual constriction. As condensation proceeds these characters become obscured until at metaphase (fig. 13) they are no longer discernible. Another species of *Aloë* showing similar constrictions in early diakinesis is shown in fig. 12. It is interesting to note here that the shorter segments of the chromosomes are attached together, while the longer segments are simply lying near and across each other.

During the anaphase of the heterotypic division the longitudinal split in each univalent chromosome becomes effective, and each univalent is usually completely separated into two halves. At this stage the constrictions obscured at metaphase become more clearly visible and are seen at the end of the univalent which travels first to the poles (figs. 24, 25). At telophase of the heterotypic division an example of the reappearance of the constriction in the chromosomes is illustrated in the single nucleus drawn in fig. 28.

Fig. 27 shows isolated chromosomes at early telophase of the heterotype division; the small chromosome figured shows both constriction and fission, giving rise to the appearance of a twofold division within the chromosome, but it is clearly only the longitudinally split univalent in which the transverse constriction has made its appearance (*cp.* TAYLOR (30)).

Chromosomes from the homotypic metaphase of *Gasteria Holtzei* are drawn in fig. 29, and fig. 30 illustrates the anaphase of this division in the same plant. The constrictions appear much more clearly in all species during the homotype division. From this it seems more probable that the obscuring during the heterotype division is due to a real condensation in the chromosomes and not due to the action of the fixative. Fig. 32 is a section of a homotypic anaphase group of a tetraploid species of *Gasteria* and shows a transverse fragmentation of the chromosomes in addition to the constrictions shown at the polar end of each chromosome. This type of fragmentation is not uncommon during the later stages, in which clear examples of constrictions in chromosomes which have not yet passed into the resting condition may be distinguished. Fig. 33 is drawn from one of the four daughter nuclei of a pollen mother-cell at early telophase.

In the division of the pollen grain nucleus the constricted ends were observed both at metaphase (Fig. 34) and during the anaphase stages.

Discussion.

It has been shown that the presence of constrictions is a constant feature in the chromosomes of the species of the four genera of the *Aloinæ* which have been examined. They are more easily observed at certain stages, but their temporary eclipse during the heterotypic metaphase is due solely to the great concentration of the chromatin at this stage. The presence of constrictions at diakinesis and at the anaphase of the second division points to the constancy of these features as part of the chromosome structure.

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As the work for this paper was nearing completion, a contribution to the cytology of *Gasteria* was published by TAYLOR (31). In the genus *Gasteria* TAYLOR failed to find any distinction either in the number or the morphology of the chromosomes in the nuclei of the species which he examined. In the individual nucleus, this investigator observed no difference between the three pairs of small chromosomes at heterotypic metaphase. He found, however, that one of the large pairs was always different from the other three, owing to the fact that the point of attachment of the spindle fibre was not terminal but at a distance from the end equal to about one-third the length of the chromosome. During the homotype division this investigator found that the three small and the three undistinguished large chromosomes have each a rounded protuberance at one end, while in the fourth large chromosome a constriction, separating a large segment from the main body of the chromosome, corresponds in position with the point of attachment of the spindle fibre during the heterotype division. At this point the spindle fibre was attached, and for the other six chromosomes the attachment lay behind a well-marked protuberance.

In a still more recent communication TAYLOR (32) gives further details concerning the structure of the chromosomes of the somatic nuclei of *Gasteria* and compares them with those of two species of *Aloë* and of a species of *Haworthia*. The results given bring to light a difference in the construction of the four pairs of large chromosomes. The variations are given by the position of the spindle fibre attachment and the presence or absence of " satellites at the distal end " of the chromosome. The variation in structure of the chromosomes forming the set for any nucleus offers a cytological basis for comparison, but apparently it is only applicable for generic distinctions. TAYLOR records no interspecific differences for the nuclei of *Gasteria* on which his more detailed work is based.

Confirmation is given in the present paper of the widespread occurrence of constrictions in the chromosomes of the *Aloinæ*, and of a variation in the position of the constrictions in chromosomes from different species, but no definite diagnostic distinction, such as that suggested by TAYLOR, has been proved from these observations. It is clear that in one chromosome of each nucleus the constriction or point of attachment is at about one-third the total length of the chromosome, but the observations on the chromosome groups of species of *Aloë* do not show that this is the structure of three of the four long chromosomes in this genus, a character which TAYLOR describes in the nuclei of *Aloë arborescens* and *Aloë saponaria*, and suggests as possibly characteristic of the genus.

The occurrence of chromosome constrictions constant in position in the univalent elements which form the bivalent chromosomes suggests the possibility of tracing the orientation of paternal and maternal chromosomes which possess such constrictions or appendages as they come out of the general spireme complex. In plants, where the weight of evidence is in favour of the origin of the bivalents by an end-to-end arrangement of the univalents, a differentiation within the chromosome would bring out more clearly

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the fact that each homologous pair must lie in such a position that the ends bearing like "genes" are together. If, in the paternal chromosome, the characters A, B, C, D, E are arranged in that order—the homologous maternal chromosome bearing the characters A′, B′, C′, D′, E′—then the arrangement of these on the spireme which gives rise to the bivalents must be E, D, C, B, A, A′, B′, C′, D′, E′ or A, B, C, D, E, E′, D′, C′, B′, A′, the next pair of chromosomes being similarly adjusted. If a "telosynapsis" interpretation of the method of evolution of the bivalent chromosome in plants is correct, and if "crossing over" of factors occurs in any such plants, then it would appear that the above arrangement must hold ("telosynapsis" and "crossing over" shown for *Lathyrus*. Punnett (21), Latter (15).) The investigation of meiosis in the *Aloinæ* is not yet completed; the prophase stages examined suggest the telosynaptic arrangement of the univalents, and stages such as those illustrated in figs. 10, 11, and 12 indicate that it may be possible, from a favourable species with such well-marked constrictions in its chromosomes, to obtain further evidence towards the solution of this vexed question.

IV. Chromosome Numbers.

A summary of the various genera and species of the Liliaceæ for which the chromosome numbers have been determined is given by Tischler (35). From this list it is seen that the most frequent haploid number in the Liliaceæ, so far as recorded, is twelve; there are several genera with eight chromosomes, several with six chromosomes, while the remaining genera afford examples of a large variety of chromosome numbers from 5 to 28 or more. The significance of these numbers has been discussed by various authors, and the basic number for the Liliaceæ is by many investigators held to be three. (Ernst (7), Newton (19), de Mol (17), etc.) Marchal (16), on the other hand, believes that four chromosomes is the original arrangement of the hereditary matter in the nucleus, and that this has remained unchanged even in some highly evolved types; all other arrangements have been derived by the duplication or loss of individual chromosomes, or transverse splitting in one or more chromosomes.

In certain families, *e.g.*, Triticum (27), the chromosome numbers do form a criterion for classification, but numbers as such have to be used with caution for classificatory purposes. Winge (36) and others have discussed this question in some detail and have pointed out that some related species have chromosomes which stand in a simple numerical relation one to another. This is true in certain genera and even in certain Natural Orders, but there are exceptions where it is difficult to see any relation between the chromatin complexes of nearly associated species.

On further analysis these may reveal some relation between the chromosome numbers and the systematic relations of the species involved, as, for example, has been shown for the genus *Carex*, in which Heilborn (13) finds no polyploid species. In this genus the chromosome numbers vary from 9 to 56, but Heilborn shows that although no series can be demonstrated for the genus as a whole, the distribution of the numbers being quite irregular, yet nearly related species possess the same or adjacent chromosome

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numbers. The origin of the higher numbers is attributed to the duplication of entire chromosomes as the result of a series of gradual changes, the higher numbers probably having been derived from the nearest lower number. Hence, if there is a basic number for the genus, it must be the lowest number in the series. At the same time it must be borne in mind that in general the chromosomes decrease in size as their number increases in the genus *Carex*.

During the course of the present research the chromosome numbers of species belonging to several genera of the Liliaceæ have been determined. The results cannot, at present, be interpreted to support the view of a basic number for the whole Natural Order Liliaceæ. In the present communication the results obtained from the subdivision *Aloinæ* only are recorded (see Table I, next page).

An examination of Table I shows that the number of chromosomes in the nuclei of the *Aloinæ* is invariably seven or a multiple of seven. A number of tetraploid species are recorded. An exact count of the small chromosomes was never obtained in *Gasteria nigricans crassifolia*, but the constitution of the nucleus and the presence of the double number of long chromosomes indicate the probability of this conclusion (see fig. 32). In the genus *Haworthia* three species are tetraploid, and in *Apicra* the species *Apicra pentagona spiralis* is tetraploid. In all the species the haploid chromosome set consists of four large and three small chromosomes, and the tetraploid plants have each group doubled, so that there are eight large and six small chromosomes at the reduction division.

Haworthia tesselata is a plant which has a number of forms. The flower-buds obtained from Mr. Horton, of Liverpool, were collected from plants of two kinds. The thick succulent leaves of the rosette were marked on the upper surface with lighter areas forming bars running longitudinally along the leaf and shorter " bars " across the leaf connecting the longitudinal bars, and so forming the tesselated appearance. In the one set of plants only two of these longitudinal bars are formed, and in the other there were constantly four bars. Subsequently, more material of *Haworthia tesselata* was obtained from the Royal Botanic Gardens at Kew. The plants there labelled *H. tesselata* have leaves 1·7 to 1·8 cm. wide at the base, and the flowering axis was 28 cm. long (in the year 1924). All the leaves had two bars, and two only, which went all the way from the base to the apex of the leaf, although frequently one more travelled part of the way over the leaf. Another variety of this species is named at Kew *H. tesselata parva*. This is a slightly larger plant than *H. tesselata*, the leaves being sometimes 3 cm. broad at the base, and the flowering axis was 55 cm. long (in the year 1924). The succulent leaves of this variety had four or five, or even as many as seven, longitudinal bars connected by the transverse markings already described.

The special interest of this species and its varieties is that, so far as could be determined from imperfectly fixed material of the two-barred form in Mr. Horton's collection, this plant is diploid, while his four-barred form and both varieties growing

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at Kew are tetraploid in their nuclear constitution. The origin of the tetraploidy is shown elsewhere (pp. 244 and 247) to be due, not to transverse segmentations in the chromatin complex of the nucleus, but to a complete duplication both in numbers and mass of the chromatin equipment of the nucleus.

TABLE I.

Genus.	Species.	Number of chromosomes in somatic (diploid) nuclei.	Haploid number of chromosomes (meiosis).
Aloë	*abyssinica*	14	7 (4 + 3)
	arborescens	14	—
	arborescens Natalensis	14	7 (4 + 3)
	Cameronii	—	7 (4 + 3)
	ciliaris	> 45	—
	cristata	—	7 (4 + 3)
	grandis	—	7 (4 + 3)
	pluridens	14	7 (4 + 3)
Gasteria	*apricoides*	(Ca) 14	—
	cheilophylla	—	7 (4 + 3)
	Cooperi	—	7 (4 + 3)
	croucheri spathulata	—	7 (4 + 3)
	excelsa	—	7 (4 + 3)
	Holtzei	—	7 (4 + 3)
	lingua	—	7 (4 + 3)
	lingua var. conspurcata	—	7 (4 + 3)
	nigricans platyphylla	—	7 (4 + 3)
	nigricans crassifolia	28	—
	retata	—	7 (4 + 3)
	rotata	14	7 (4 + 3)
Haworthia	*Cooperi*	—	7 (4 + 3)
	cymbiformis	—	7
	hybrida	14	7 (4 + 3)
	glabrata	—	7 (4 + 3)
	glabra pervivida	—	7 (4 + 3)
	lævis	—	7 (4 + 3)
	pseudotortuosa	—	14 (8 + –)
	rigida	14	—
	recurva	—	7 (4 + 3)
	radula	—	7 (4 + 3)
	subfasciata	28 (?)	—
	tesselata (Mr. HORTON)—		
	2 bars	14	—
	4 bars	28	—
	tesselata KEW	28	—
	tesselata parva KEW	—	14 (8 + 6)
Apicra	*aspera*	—	7 (4 + 3)
	deltoidea.	14	7 (4 + 3)
	pentagona spiralis	—	14 (8 + 6)

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V. Chromosome Size and Measurement.

The qualitative distinction between large and small chromosomes in the nuclei of plants has long been recognised. The earliest record of the unequal size of the chromosomes in a single nucleus was made by Strasburger (1882) for *Hosta Sieboldiana*. Similar inequalities in chromosome size have been found in the nuclei of many monocotyledonous plants, and are now known to occur also in Dicotyledons and among Gymnosperms. Reviews of the literature and summaries of the results hitherto obtained are given by Müller (18) and Tischler ((35), p. 610).

Quantitative measurements of the size of the chromosomes in plants are comparatively few. Müller (18) determined the actual lengths of the chromosomes at the somatic metaphase of a number of species of both Monocotyledons and Dicotyledons. In a critical paper by Farmer and Digby (8) the measurement of the *widths* of the chromosomes in certain phyla of plants, as well as in a number of animal nuclei, are given to test Meek's thesis that chromosome width is an indication of phylogenetic affinity in the animal kingdom, and that it is "correlated with the order of phylogeny." These authors find that the evidence in no way supports Meek's proposition. The chromosome lengths are given by Farmer and Digby only for species of *Primula*, the volume of whose chromatin content was calculated.

In addition to these measurements, absolute chromosome lengths have been determined in a few genera of plants. For example, Rosenberg (24) demonstrates the size relations between the various chromosomes of a 4-chromosome and a 3-chromosome species of *Crepis*, proving that for *Crepis Reuteriana*, if the chromosome lengths are represented by *a*, *b* and *c*, *Crepis tectorum* has, in addition to *a*, *b* and *c*, a fourth chromosome equal in size to *c*.

A detailed series of measurements has been made by Heilborn (13) for three species of *Carex*. This author finds that the chromosome lengths of the long, medium-sized, and short chromosomes which appear in different numbers in the nuclei of the various species have a fairly constant value for any one species. In *Carex pilulifera* and *Carex panicea* the sum of the lengths of the middle-sized and short chromosomes is equal to the length of the long chromosome, but the long and medium chromosomes are shorter in *C. panicea* than in *C. pilulifera*. This difference is not regarded by Heilborn as a feature of any importance, although the short chromosomes of the two species are given as almost exactly equal in length.

Methods of Measurement of Chromosomes.

The methods which have been used for the quantitative measurement of chromosomes can generally be grouped under two headings.

(1) *Direct Measurement with Ocular Micrometer.*—Müller's (18) determinations were made in this way, and for chromosomes which lie evenly in the field this method gives an approximate result rapidly. Details are given by Terby (34), who used an ocular

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micrometer with divisions of 1/20 mm., for the measurement of the chromosomes of *Butomus*. TERBY states that measurements were only attempted when the chromosomes lay wholly lengthwise in the equatorial plate, and that out of 20,000 sections, 4 figures only allowed the exact measurement of *all* its chromosomes. This illustrates the difficulty which may be met in attempting to obtain accurate values for the chromosome size.*

(2) *The Second Method* which has been employed is to draw the chromosomes with the aid of a camera lucida. ROSENBERG (24) used squared mm. paper and so obtained his values directly, knowing the magnification. He also obtained relative values by enlarging drawings made on transparent paper by means of a projection apparatus and measuring the enlarged image with a planimeter. HEILBORN (13) similarly drew the chromosomes of Carex with the aid of a camera lucida, and measured the drawings, using a low-power microscope, thus obtaining a magnification of 4,000 diameters. DE MOL (17) used an ingenious method for measuring the lengths of chromosomes drawn with the camera lucida. By means of a number of discs of aluminium having a diameter equal to the mean width of the chromosomes, which DE MOL found to be the same for all, and counting the number of discs necessary to cover the chromosomes, he obtained the relative lengths of the short, medium and long chromosomes in species and varieties of *Hyacinthus*.

For the measurements, the results of which are presented in this communication, outline drawings of the chromosome groups were made, using a camera lucida, at a magnification of 3,000 diameters. The dimensions of the individual chromosomes were then taken by means of finely pointed dividers; the lengths were read off on a millimetre scale, estimating the value to the nearest tenth of a millimetre. The dimensions obtained in this way in millimetres from the drawings were tabulated. The tables giving the actual sizes of the chromosomes were obtained from these by dividing by the magnification (3000) and reducing the observations so that the actual dimensions of the chromosomes are given in terms of μ (1×10^{-3} mm.).

Results.—MÜLLER (18) gives the measurements of the lengths of the chromosomes in the somatic nuclei of a number of plants belonging to the Natural Order Liliaceæ. Among these is a species of *Aloë*—*Aloë Hanburyana*—and of the 14 somatic chromosomes he finds that 4 pairs are 15–16 μ long, one pair 6 μ long, 2 pairs are 4 μ long, all being about 2 μ broad.

In the following account details of the size of chromosomes in 10 species of the sub-division *Aloinæ* are given.

A. Chromosome Lengths.—Table II is a specimen of the tables obtained for all the species measured, and gives the particulars of the measurements in length of each

* The magnification is not given by TERBY, and where the chromosomes cover, for example, 6 divisions in the eyepiece, the length of the chromosome is given as 300 μ. This is clearly not the actual size of the chromosome, but the size as viewed under the microscope with that particular magnification. It is obviously essential, if the numerical figures are to be of value for comparative work, to know the actual size of the chromosomes, and for this the magnification, as well as the observed magnified dimensions, should be given.

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chromosome from the drawings made in the way already described. This table gives the magnified lengths of the chromosomes of *Aloë arborescens Natalensis*. Each horizontal series of seven numbers gives the lengths of the seven chromosomes contained in any one nucleus. The vertical columns represent chromosomes from different nuclei. The lengths are given in millimetres. All the chromosomes included in Table II are from nuclei at heterotypic metaphase (fig. 14) in polar view, unless it is otherwise stated.

TABLE II.—*Aloë arborescens Natalensis*.

Stage.	Magnified lengths of chromosomes in millimetres.						
Heterotypic metaphase	15·0	14·0	18·0	19·0	6·0	6·3	6·0
	16·5	16·0	15·0	—	6·0	6·0	6·0
	15·5	20·0	16·0	15·5	7·0	6·0	6·5
	18·0	14·0	—	15·0	6·0	7·0	5·0
	14·5	17·5	15·0	14·5	6·2	5·5	6·0
	17·0	15·0	—	—	6·0	5·5	6·0
	16·2	18·5	15·2	15·5	7·0	5·5	6·2
	16·0	15·5	15·0	—	6·0	5·5	4·5
	15·0	18·0	—	—	6·0	4·5	6·0
	—	17·0	15·2	17·0	7·5	6·0	6·2
	15·0	16·0	16·2	14·0	7·5	6·5	5·5
	15·0	15·0	15·2	17·0	6·2	6·0	6·0
	17·0	18·0	23·5	17·2	9·0	8·0	7·0
	19·2	—	18·3	14·5	6·0	7·0	7·0
	—	—	—	18·0	7·0	5·5	5·5
Heterotypic metaphase in profile.	17·0	21·5	13·5	16·2	7·5	6·0	7·0
	20·5	19·0	—	—	6·5	6·0	5·2
Heterotypic anaphase	16·5	13·0	9·0	17·5	5·5	5·0	6·2
	12·5	10·2	18·5	—	5·0	—	—
	17·0	15·0	15·0	11·7	4·5	8·5	3·5
Homotypic chromosomes	12·0	14·0	11·5	12·2	7·5	6·0	7·5

Table III gives the actual size of the chromosomes of the nuclei of *Aloë arborescens Natalensis* in terms of μ (derived directly from Table II).

Table V gives a summary of all the measurements obtained for the lengths of the chromosomes in the ten species hitherto examined. It is a frequency table, the results of the measurements being grouped in classes to the nearest 0·5μ (that is, those from 1·3μ to 1·7μ are classed under 1·5μ, those from 1·8μ to 2·2μ under 2μ, etc.), and the number of chromosomes of any given size is recorded for each species. Thus, of the short chromosomes of *Aloë arborescens Natalensis*, for which the stages of the determination have been detailed, at the metaphase of the heterotype division 5 chromosomes have a length of 1·5μ, 33 chromosomes have a length of 2μ, 13 have a length of 2·5μ, and 1 has a length of 3μ. Similarly, for the longer chromosomes, 3 measure 4·5μ, 20, 5·0μ; 14, 5·5μ; 8, 6·0μ; 5, 6·5μ; 2, 7μ; and 2, 8μ in length.

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TABLE III.—*Aloë arborescens Natalensis.*

Stage.	Lengths of chromosomes in μ.						
Heterotypic metaphase	5·0	4·7	6·0	6·3	2·0	2·1	2·0
	5·5	5·3	5·0	—	2·0	2·0	2·0
	5·2	6·7	5·3	5·2	2·3	2·0	2·2
	6·0	4·7	—	5·0	2·0	2·7	1·7
	4·8	5·8	5·0	4·8	2·0	1·7	2·0
	5·7	5·0	—	—	2·0	1·8	2·0
	5·4	6·2	5·1	5·2	2·3	1·8	2·1
	5·3	5·2	5·0	—	2·0	1·8	1·5
	5·0	6·0	—	—	2·0	1·5	2·0
	—	5·7	5·1	5·7	2·5	2·0	2·0
	5·0	5·3	5·4	4·7	2·5	2·2	1·8
	5·0	5·0	5·1	5·7	2·1	2·0	2·0
	5·7	6·0	7·8	5·7	3·0	2·7	2·3
	6·4	—	6·1	4·8	2·0	2·3	2·3
Heterotypic metaphase in profile	5·7	7·2	4·5	5·4	2·5	2·0	2·3
	6·8	6·3	—	—	2·2	2·0	1·7
Heterotypic anaphase	5·5	4·3	3·0	5·8	1·8	1·7	2·1
	4·2	3·4	6·2	—	1·7	—	—
	5·7	5·0	5·0	3·9	1·5	2·8	1·2
Homotypic chromosomes	4·0	4·7	3·8	4·1	2·5	2·0	2·5

TABLE IV.—Frequency Table of Lengths of Chromosomes in *Aloë arborescens Natalensis.*

Length in μ	1·5	1·7	1·8	2·0	2·1	2·2	2·3	2·5	2·7
Number of chromosomes	2	3	6	21	3	3	7	4	2

Length in μ	2·8	3·0	—	4·5	4·7	4·8	5·0	5·1	5·2	5·3	5·4
Number of chromosomes	0	1	—	1	2	3	10	3	4	4	3

Length in μ	5·5	5·7	5·8	6·0	6·1	6·2	6·3	6·4	6·7	6·8	7·2	7·8
Number of chromosomes	1	6	1	5	1	2	2	1	2	1	1	2

The results tabulated in Table V are represented graphically in the text-figure. The discontinuity of the curves shows the sharp differentiation in the sizes of the chromosomes in this group. Both from the graphs and the measurements already given, it is clear that there is no overlapping in the sizes of the large and small chromosomes.

Table VI gives the average lengths of the long and of the short chromosomes, taken separately, at the heterotype metaphase. From this table as from the graph in the above figure, a comparison of the lengths of the shorter chromosomes shows

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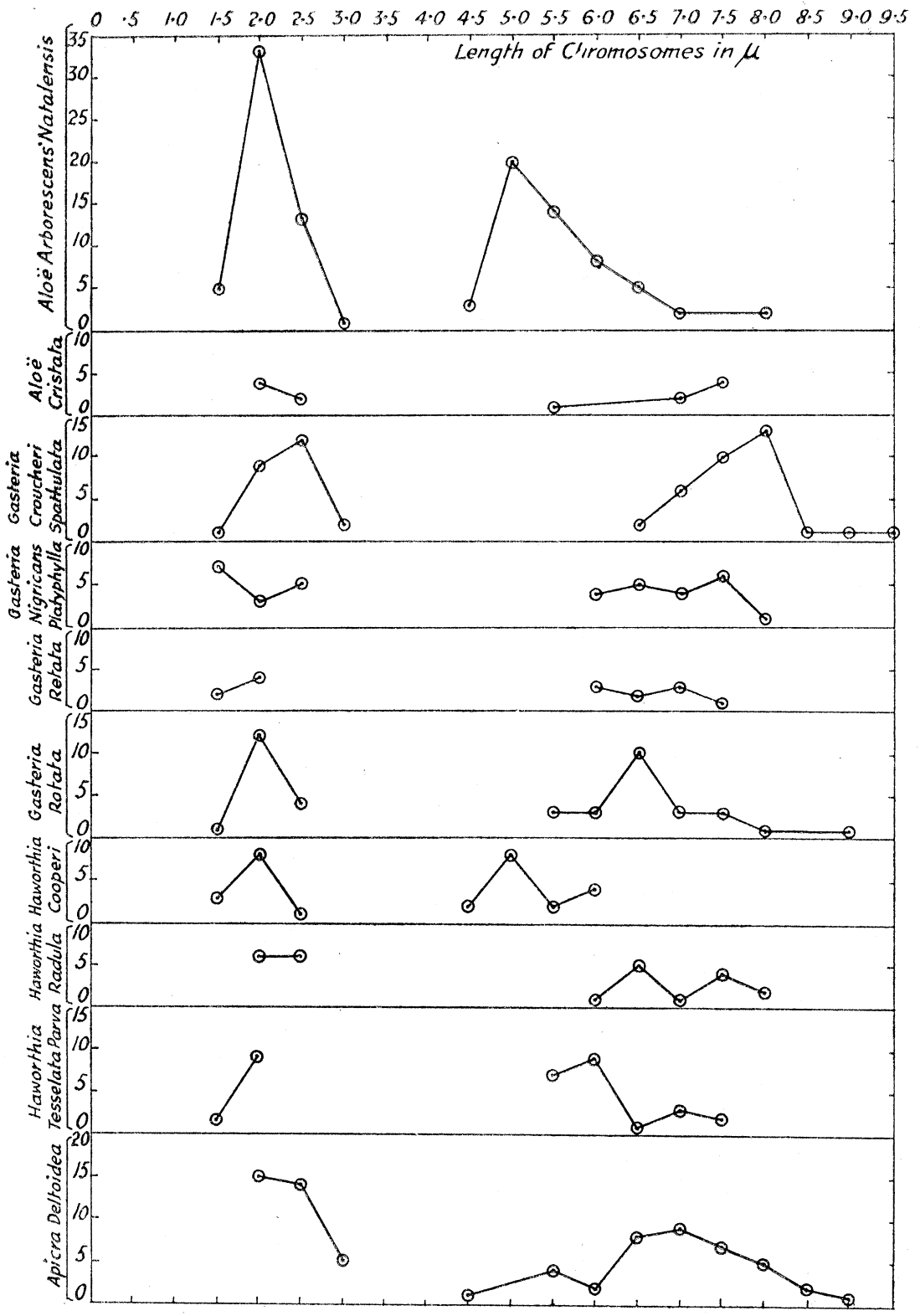

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only a small amount of variation in the size of these bodies, 1·8μ and 2·4μ being the extreme values of the average lengths. The average lengths of the long chromosomes

TABLE V—Summary of the Measurements of the Lengths of Chromosomes in the Heterotype Division at Metaphase.

Species.	Lengths of chromosomes in μ.																
	1·5	2·0	2·5	3·0	3·5	4·0	4·5	5·0	5·5	6·0	6·5	7·0	7·5	8·0	8·5	9·0	9·5
Aloë arborescens Natalensis . . .	5	33	13	1	—	—	3	20	14	8	5	2	—	2	—	—	—
*Aloë cristata** . . .	—	4	2	—	—	—	—	—	1	—	—	2	4	—	—	—	—
Gasteria Croucheri spathulata . . .	1	9	12	2	—	—	—	—	—	—	2	6	10	13	1	1	1
Gasteria nigricans platyphylla . . .	7	3	5	—	—	—	—	—	—	4	5	4	6	1	—	—	—
Gasteria retata . . .	2	4	—	—	—	—	—	—	—	3	2	3	1	—	—	—	—
Gasteria rotata. . .	1	12	4	—	—	—	—	—	3	3	10	3	3	1	—	1	—
Haworthia Cooperi .	3	8	1	—	—	—	2	8	2	4	—	—	—	—	—	—	—
Haworthia radula† .	—	6	6	—	—	—	—	—	—	1	5	1	4	2	—	—	—
Haworthia tesselata parva†	2	9	—	—	—	—	—	—	7	9	1	3	2	—	—	—	—
Apicra deltoidea . .	—	15	14	5	—	—	1	—	4	2	8	9	7	5	2	1	—

* Fixed in CARNOY'S fluid.

† Fixed in ALLEN'S modification of BOUIN'S mixture.

TABLE VI.—Average Lengths of the Long and Short Chromosomes at Heterotypic Metaphase.

Species.	Average length of long chromosomes.	Average length of short chromosomes.
Aloë arborescens Natalensis	5·5 μ	2·0 μ
Gasteria Croucheri spathulata . . .	7·7 μ	2·3 μ
Gasteria nigricans platyphylla . . .	6·9 μ	1·9 μ
Gasteria retata	6·8 μ	1·8 μ
Gasteria rotata	6·7 μ	2·1 μ
Haworthia Cooperi	5·3 μ	1·9 μ
Haworthia radula	7·0 μ	2·4 μ
Haworthia tesselata parva	6·3 μ	1·9 μ
Apicra deltoidea	7·0 μ	2·4 μ

vary from 5·3μ for *Haworthia Cooperi* to 7·7μ for *Gasteria Croucheri spathulata*, a difference of 2·4μ, which seems of some significance. It is felt that the measurements must be determined for a wider number of species before any generalised conclusion can be made.

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The fact that the lengths of the chromosomes of any one species tend to group themselves round two very different values, a fact which is shown also by the drawings, is emphasised by the results obtained on measuring the chromosomes. In all species of the *Aloinæ*, the lengths of the chromosomes fall into two classes, the smaller-sized chromosomes being most frequently about 2μ long, the larger varying from 5μ to 9μ in length. The methods of microdissection have shown that chromosomes may be easily stretched and deformed (CHAMBERS and SANDS (3)), so that a certain amount of irregularity is inevitable, due to the plastic nature of these bodies acted upon as they are by unknown but undoubted forces in the cell. Nevertheless, when the chromosomes are taken at the same stage of division, the forces acting are probably comparable in cells of the same species, and the measurements show that a mean exists (in the ordinary sense of the word "mean"), which may be taken as a measure of the length of the chromosomes peculiar to any given species. There is, as far as the observations go, no appreciable skewness in the frequency curves, the scattering apparently following the ordinary law of error.

It has already been pointed out that the lengths of the short chromosomes in all the examined species are very uniform; variation in length is found, however, when the long chromosomes of one species are compared with those of another. In *Aloë arborescens Natalensis* the long chromosomes are considerably shorter than those, for example, of *Gasteria Croucheri spathulata*, while the measurements given for the three species of *Haworthia* show that there is a distinction in length between the most frequent length peculiar to each species.

The writer gives these results, tentatively suggesting that lengths of chromosomes (or total chromosome volume) *may* be a specific diagnostic character in a group such as the *Aloinæ*, in which there is such a remarkable uniformity in the general structure of the nucleus during its division.*

B. Chromosome Width and Depth Measurements.—Table VII is a summary of the widths and depths of the chromosomes of the species of the *Aloinæ* whose length measurements have already been discussed. The table is a frequency table arrived at in a similar way for the width and depth measurements as Table V was for length measurements. The figures show a wide range of variation in the width measurement of chromosomes in the one species, and it was found that, especially in the large chromosomes, a considerable variation may occur in the width at different parts of the same chromosome. (See also figs. 14–20.) The last vertical column gives the average width for the species and stage indicated in the horizontal column. Thus the first line of results shows, for *Aloë arborescens Natalensis*, that the univalent width of 13 chromosomes is 1·0μ, of 121 chromosomes 1·5μ, of 61 chromosomes 2·0μ, of 13 chromosomes 2·5μ, while the average width from all the measurements is 1·7μ (which is not very different from the mode).

FARMER and DIGBY (8) clearly demonstrated a variation in the value of the width of

* TAYLOR (31) could not in any way distinguish between the nuclei of various species of *Gasteria* which he examined.

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TABLE VII.—Summary of Measurements of the Widths and Depths of Chromosomes during Meiosis.

Species.	Stage measured.	Frequency table of widths and depths.									Average width or depth in μ.
		0·5μ	1·0μ	1·5μ	2·0μ	2·5μ	3·0μ	3·5μ	4·0μ	4·5μ	
Aloë arborescens Natalensis	Univalent width	—	13	121	61	13	—	—	—	—	1·7
	Bivalent width	—	—	3	14	14	29	14	5	3	2·9
	Depth (from profile spindles)	—	10	24	11	5	2	—	—	—	1·6
	Anaphase 1 (width of ½ univ.)	1	11	36	1	—	—	—	—	—	1·4
	Metaphase 2	—	4	9	6	1	—	—	—	—	1·6
Aloë cristata	Univalent width	—	—	4	14	9	2	—	—	—	2·1
	Bivalent width	—	—	—	1	4	4	—	—	—	[2·7]
Gasteria Croucheri spathulata	Univalent width	—	1	30	35	12	2	—	—	—	1·9
	Bivalent width	—	—	—	5	22	44	33	16	3	3·2
	Depth (from profile spindles)	—	—	—	—	2	5	4	3	—	[3·3]
Gasteria nigricans platyphylla	Univalent width	—	1	18	15	6	1	—	—	—	1·9
	Bivalent width	—	—	—	—	—	5	6	1	—	3·3
	Depth (from profile spindles)	—	—	12	—	—	—	—	—	—	[1·5]
	Ana. 1 (width of ½ univ.)	2	30	22	—	—	—	—	—	—	1·2
Gasteria retata	Univalent width	—	2	18	2	—	—	—	—	—	1·5
	Depth from profile spindles	—	1	8	5	1	—	—	—	—	1·7
Gasteria rotata	Univalent width	—	1	24	43	12	—	—	—	—	1·8
	Bivalent width	—	—	—	4	9	3	4	1	—	2·7
Haworthia Cooperi	Univalent width	—	13	35	8	1	—	—	—	—	1·4
	Bivalent width	—	—	—	5	4	8	4	5	—	3·1
Haworthia radula	Univalent width	—	—	13	34	11	1	—	—	—	2·0
	Bivalent width	—	—	1	8	8	7	5	—	1	2·6
Haworthia tesselata parva	Univalent width	—	4	27	50	33	2	—	2	—	2·1
	Bivalent width	—	—	—	—	1	1	1	—	—	[3·0]
Apicra deltoidea	Univalent width	—	1	25	40	18	4	1	—	—	2·0
	Bivalent width	—	—	6	11	23	21	14	6	—	2·7
	Depth (from profile spindles)	—	—	20	20	2	1	—	—	—	1·8
	Ana. 1 (width of ½ univ.)	—	1	14	6	—	—	—	—	—	1·5

the chromosomes in both animals and plants. In the member of the Liliaceæ described by them, namely *Galtonia*, these investigators found a difference in width between the small and large chromosomes, although each showed a small range of variation. In the *Aloinæ* the range of variation is much greater, and it was found that there was so much

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overlapping in the measurements of the widths of small and large chromosomes that all the results have been treated together in this table, although the small chromosomes are, on the whole, slightly narrower than the large ones. Possibly they are slightly deformed, due to the fact that the univalents of the smaller bivalents are already separated and lie along the length of the spindle at the stage when the larger bivalents lie with their univalent segments in the equatorial plate.

From Table VII the following results emerge :—

(1) The width of the univalent chromosome at heterotypic metaphase shows a range of variation, but the most frequent width is $1 \cdot 5 \mu$ to $2 \cdot 0 \mu$, and all the average values for the width lie between the limits $1 \cdot 4 \mu$ and $2 \cdot 1 \mu$.

(2) The depth measurements from drawings of heterotypic spindles seen in profile give $1 \cdot 5 \mu$ as the most frequent value for this dimension.

(3) Where the univalent chromosomes were closely pressed together or twisted about each other so that the width of the univalent segments could not clearly be seen, the width of the closely paired univalents was measured and, as might be expected from the fact that the degree of association varies, there is considerable variation in the value of the width, but on the whole the most frequent bivalent width is a little less than double the univalent width in the same species.

(4) Whenever there is a release between the longitudinally associated chromosomes or portions of chromosomes there is a readjustment of shape in the chromosomes. Thus the closely associated pairs of univalents in any one species show a width less than twice the width of the univalents in the same species when the lateral association is broken and the univalents lie separately. Further, in the species now under discussion, it was found that very early after the separation of the univalents, in some instances before this separation is completed (*v.* fig. 22) the univalent chromosomes are already split, and this split is usually completely effected before the poles of the spindle are reached. Measurements of these split halves of the univalent chromosomes during the anaphase of heterotype division show that although the widths are considerably less than those of the univalent chromosomes, yet they are much more than half the width of the univalent, of which each is a longitudinal half. These stages rapidly succeed each other, and presumably there is little or no growth, or addition of material in such an active state. These results supply further evidence of the plasticity and fluid nature of the chromosomes, and it is suggested that when the bivalents separate into their univalent segments each segment on release, owing to the surface forces, tends to take up a cylindrical shape. For the purpose of this argument it is assumed that the length remains practically constant, and this is borne out by the measurements, so that in order to test the accuracy of the suggestion, all we are concerned with are the ratios of the cross-sectional areas of the chromosomes. If the assumption that at each stage the chromosomes are roughly cylindrical is correct, then, if R_1 be the radius of the bivalent, its cross-sectional area $= \pi R_1^2$, or if D_1 is the measured width of the chromosomes, the cross-sectional area $= \frac{1}{4}\pi D_1^2$.

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Similarly, if D_2 is the measured width of the univalent chromosome, its cross-sectional area will be $\frac{1}{4}\pi D_2^2$, and if the split halves of the univalents as measured in heterotype anaphases have a width D_3, their cross-sectional area is $\frac{1}{4}\pi D_3^2$.

Hence, if the chromosomes consist of non-expansible substance and do not suffer distortion owing to external forces, so that their lengths may be taken as constant throughout the process, then

$$\frac{\pi}{4} D_1^2 = 2\left[\frac{\pi}{4} D_2^2\right] \quad \text{and} \quad \frac{\pi}{4} D_2^2 = 2\left[\frac{\pi}{4} D_3^2\right]$$

or

$$D_1^2 = 2D_2^2 = 4D_3^2 \quad \text{and} \quad D_1 = \sqrt{2}D_2 = 2D_3.$$

In order to test this, the average values of the widths at these stages are taken from Table VII.

TABLE VIII.

Species.	D_1	D_2	D_3	D_1	$\sqrt{2}D_2$	$2D_3$
Aloë arborescens Natalensis . . .	2·9 μ	1·7 μ	1·4 μ	2·9	2·4	2·8
Gasteria nigricans platyphylla . .	3·3 μ	1·9 μ	1·2 μ	3·3	2·7	2·4
Apicra deltoidea	2·7 μ	2·0 μ	1·5 μ	2·7	2·8	3·0

Although the results do not show absolute agreement between the values of D_1, $\sqrt{2}D_2$, and $2D_3$, they are sufficiently close to justify the assumption that there is a rapid change of shape as the result of the action of surface forces on the chromosome, when separation of univalents, or splitting of univalents, takes place.

C. Volume of Chromatin in the Nucleus.—For the calculation of the volume of chromatin in the nucleus, the average values for the length and width are employed. If w is the average width for the species, and L_1 is the average length of the long chromosomes, while L_2 is the average length of short chromosomes, then volume

$$V = 4\pi\left(\frac{w}{2}\right)^2 L_1 + 3\pi\left(\frac{w}{2}\right)^2 L_2$$

$$= \frac{\pi w^2}{4}(4L_1 + 3L_2) = \frac{\pi w^2}{4} L,$$

where L is the total length of the chromosomes in the nucleus.

The volume of the chromosomes, as indicated in these results, shows a large variation in the value of this quantity among the species of the *Aloinæ*. The tetraploid species *Haworthia tesselata parva* is included in the table (here there are 8 long chromosomes and 6 short ones; a † marks the figures to which this duplication applies). The volume of chromatin in this species is clearly of the order of *twice* the volume of the chromatin even of the diploid species with the maximum amount of chromatin in their nuclei.

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D. Discussion and Conclusions.—The actual size of chromosomes appears to offer assistance to the Biologist, in the first place, possibly as a specific diagnostic character, although sufficient data are not as yet available to establish this principle. The data offered in this paper indicate that a difference of size does occur between chromosomes of related species. This is true of the species of the *Aloinæ* which have been examined from this point of view, but there is evidence that it is not generally true, for NEWTON* (19) finds for the genus *Galtonia* that "In number and relative length the chromosomes of *Galtonia princeps* are identical with those of *Galtonia candicans*. There is no difference in width between the chromosomes of the various groups in either plant."

TABLE IX.

Species.	Average length of chrs. in μ.							
	L_1.	L_2.	$4L_1$.	$3L_2$.	L.	*w*.	Log V.	V in μ^3.
Aloë arborescens Natalensis	5·5	2·0	22·0	6·0	28·0	1·7	1·7920	61·9
Gasteria Croucheri spathulata.	7·7	2·3	30·8	6·9	37·7	1·9	2·0179	104·2
Gasteria nigricans platyphylla.	6·9	1·9	27·6	5·7	33·3	1·9	1·9640	92·0
Gasteria retata.	6·8	1·8	27·2	5·4	32·6	1·5	1·7494	56·2
Gasteria rotata.	6·7	2·1	26·8	6·3	33·1	1·8	1·9144	82·1
Haworthia Cooperi	5·3	1·9	21·2	5·7	26·9	1·4	1·6060	40·4
Haworthia radula.	7·0	2·4	28·0	7·2	35·2	2·0	2·0325	107·7
Haworthia tesselata parva†.	6·3	1·9	50·4†	11·4†	61·8†	2·1	2·3194	208·6†
Apicra deltoidea	7·0	2·4	28·0	7·2	35·2	2·0	2·0325	107·7

Secondly, quantitative measurements of chromosome size should act as a method of verifying any speculations as to the relation and origin of chromosome numbers in related species of plants. For example, DE MOL (17) brings forward evidence to show that in species of *Hyacinthus* where the chromosomes are of 3 lengths, *a*, *b* and *c*, that

$$b + c = a.$$

Thus, as in the 8-chromosome varieties with 4 long, 2 medium and 2 short chromosomes, DE MOL derives these plants with unequal chromosomes from plants whose nuclei contained 3 (or some multiple of 3) chromosomes of equal length. On the other hand, the lengths of the chromosomes of *Galtonia* do not, as NEWTON (19) points out, permit of any such interpretation of the origin of this genus from such a standardised ancestor.

As an illustration of increase in numbers of chromosomes by a different method, ROSENBERG'S measurements for species of *Crepis* may be taken (24). He shows that the 4-chromosome species *Crepis tectorum* differs from the 3-chromosome species *Crepis*

* NEWTON does not state whether his conclusion is based on quantitative measurements of the chromosome size.

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Reuteriana in the presence of a fourth chromosome equal in size to the smallest of the three chromosomes of *Crepis Reuteriana*. A small number of measurements only are given, but these all support this contention. It is not easy to say which of the species are nearer the ancestral type, but there is undoubted evidence for ROSENBERG's conclusion "dass die 3-4-5 Serie der *Crepis*-Arten etwa durch Unregelmässigkeiten während der Reductionsteilung, wie oben angegeben, zu erklären ist, und zwar auf Grund des Auftretens von konstanten Proportionen innerhalb der Chromosomengarnitur der untersuchten Arten. Die verschiedenen Chromosomenzahlen in dieser Gattung sind also nicht durch eine Querteilung eines grossen Chromosoms entstanden. Die Konstanz der relativen Chromosomengrössen spricht entschieden dagegen." COLLINS and MANN (4A), also dealing with *Crepis*, state that in *Crepis biennis*, with its 20 pairs of chromosomes, the chromosomes are similar in breadth and length to those of most of the other species, so that the greater number must have resulted from a duplication and not from a transverse division of the chromosomes.

In the genus *Carex*, to which reference has already been made (p. 11), HEILBORN (13) finds no evidence to support the thesis of the origin of the high-numbered chromosome species by transverse segmentation of a few original long chromosomes, although a transverse division of a long chromosome to form a medium and a short chromosome probably took place when the original fundamental set of the genus was formed. In this genus the evidence suggests that the higher number of chromosomes has arisen as the result of a duplication of particular chromosomes.

In the *Aloinæ*, with the exception of tetraploid species, all the species examined contain four large and three small chromosomes as the haploid number. Numerically there is no variation; in this group of plants it is the length of the chromosomes which is different in the different species.

Another question, to the solution of which a comparison of the size of the chromosomes of related species gives a clue, is the origin of tetraploidy in certain genera. This question has been discussed (12), but hitherto little attention has been paid to the accurate determination of the size of the chromosomes of the diploid and tetraploid species. The origin of one tetraploid species is, however, proven.

FARMER and DIGBY (8), by means of a series of measurements of the chromosomes of the tetraploid fertile form of *Primula Kewensis*, showed that the chromatin content of the nuclei in these plants was equal to that in the nuclei of the sterile hybrid, which is diploid. Hence they conclude that the increased number of the fertile plant has been arrived at by a transverse fission of each chromosome in the diploid form. The origin of tetraploidy in *Primula Kewensis* is therefore clear, the results being obtained from the diploid parent and its tetraploid derivative.

The ancestry of the tetraploid species *Haworthia tesselata parva* (Kew) is not known, so that the size of the chromosomes in this species and the volume in each nucleus can only be compared generally with other species from the same and the closely allied genera. At the metaphase of the heterotype division there are, in *Haworthia tesselata parva*

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(Kew) eight large bivalent chromosomes and six smaller bivalent chromosomes (Plate 19, fig. 18) compared with four large and three small bivalent chromosomes in the majority of the observed species.

Reference to Tables V, VI and VII show that in length and width the chromosomes of this tetraploid species are of the same order of magnitude as those of the majority of the diploid species, while in Table IX the fact is abundantly clear that there is in the nuclei of this species twice the volume of chromosome material found in the nuclei of any of the diploid species. Hence, measurements show that in this instance the tetraploid condition has, in all probability, been derived, not by a transverse division of the chromosomes, but by a duplication of the entire chromatin complex of the nucleus.

Probably both methods have frequently occurred in the origin of tetraploid plants, although hitherto few figures giving the comparative sizes of the chromosomes in diploid and tetraploid forms have been available.

In *Œnothera gigas* the implication appears to be that the chromosome set of *Œ. Lamarckiana* has been completely duplicated in the tetraploid mutant (10), (11).

A similar duplication is claimed by Clausen and Goodspeed (4) to be the origin of a hexaploid form of *Nicotiana glutinosa* × *N. tabacum*, *var. purpurea*, a single fertile hexaploid plant among a sterile population of F_1 hybrids which were all triploid.* Clausen and Goodspeed hold that the original fertile plant which arose among an otherwise sterile generation owes its fertility to "a doubling of the chromosome number immediately or soon after fertilization by which a tetraploid hybrid with 36 pairs of chromosomes was produced." The origin of the "tetraploidy" would, therefore, be the same as that suggested for *Œnothera gigas*.

These authors criticize the conclusions of Farmer and Digby (8) (see p. 246) with respect to the origin of the fertile *Primula Kewensis*, and suggest for this plant an origin similar to that which they assume for their fertile hexaploid F_1 hybrid of *Nicotiana*. The evidence of the exact volume measurements given by Farmer and Digby is apparently neglected.

Clausen and Goodspeed give no measurements in support of their own hypothesis that the origin of the hexaploid form of *Nicotiana glutinosa* × *tabacum* is the result of duplication of each chromosome set obtained from the original parents of the hybrid. A measurement of the chromosomes figured does not support, even approximately, the idea of uniformity of size between the chromosomes of the nuclei of the sterile F_1 hybrid and those of the fertile hexaploid plants. No stress can be laid on this, however, since "Fig. 1 was drawn from fixed material, the other two figures from

* Clausen and Goodspeed (4) apply the term "tetraploid" to the fertile hybrid *N. glutinosa* × *tabacum*. According to the present convention, *N. tabacum* with 24 chromosomes in the gametic cells is the tetraploid species. The typical sterile hybrid *N. glutinosa* × *tabacum* is, therefore, a triploid form, while the fertile hybrid should be regarded as a *hexaploid*, not a *tetraploid*, member of the series. Similar triploid sterile hybrids are not uncommon; *cp.* the well-known sterile hybrid *Drosera longifolia* × *D. rotundifolia* (23), the hybrids between diploid and tetraploid species of *Callitriche* (14), etc., although no fertile hexaploid has as yet been observed to arise from these triploid hybrids.

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acetocarmine preparations"; although, if the magnification is the same, the presumably swollen chromosomes of the acetocarmine preparations of the hexaploid nuclei are, as figured, appreciably smaller than those of the fixed material of the triploid form.

Exact quantitative measurements of the chromosomes from fertile and sterile hybrids whose anthers have been fixed under conditions as nearly uniform as possible would, as has been emphasised previously in this communication, help to elucidate the question of the origin of hexaploidy in this species hybrid.

Another example is given by *Datura* with its 12 haploid chromosomes, which fall into six size-classes, and in this genus BELLING and BLAKESLEE (2) indicate that the diploid, triploid, and tetraploid forms have nuclei which contain 2, 3 and 4 sets respectively of these chromosomes in their entirety. In the absence of exact measurements it is not safe to speculate, but if the above is true, tetraploidy in *Œnothera gigas*, in *Datura* and in *Haworthia tesselata parva*, has probably been arrived at by some similar mechanism, which is totally different from that which has brought about the same *numerical* duplication in the chromosomes in *Primula Kewensis*.

SUMMARY AND CONCLUSIONS.

1. The cytology of certain genera of the *Aloinæ*—*Aloë*, *Gasteria*, *Haworthia* and *Apicra*—forms the subject of this communication. The plants are xerophytic, occurring mainly in South Africa. All the genera are examples of a very uniform "growth form."

2. The occurrence of constrictions is a constant feature of the chromosomes of the *Aloinæ*. These constrictions are generally obscured during heterotypic metaphase, but they have been observed in late prophase, in anaphase and telophase, of the heterotypic division, and during the homotypic division, as well as in the chromosomes of somatic nuclei.

It is suggested that the obscuring of the constriction at heterotypic metaphase is due to the fact that the chromosomes reach their maximum condensation at this stage. The point of attachment of the spindle fibres is at the constricted portion of the chromosomes. The constrictions are subterminal, but the distance from the end of the chromosome is not constant for all the chromosomes in a nucleus; the length of the arm beyond the constriction is always greater in at least one of the large chromosomes of a set than in the other three.

It is suggested that a detailed study of the prophase of meiosis in a species with well-marked constrictions would give further evidence concerning the orientation of the bivalent chromosomes in the spireme. From the present research a telosynaptic arrangement of the univalents is strongly suggested.

3. The haploid number of chromosomes in all genera of the *Aloinæ* is *seven*—with fourteen in the tetraploid species. These chromosomes are of unequal size—four large and three small chromosomes in each nucleus. No conclusions are drawn concerning the origin of this arrangement of the chromatin from any of the arrangements, hitherto suggested for the Liliaceæ, of the ancestral equipment of the nucleus.

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4. The dimensions of the chromosomes of species of each of the four genera of the *Aloinæ* were determined by measuring highly magnified outline diagrams of the chromosomes drawn with the aid of a camera lucida.

From the results it is suggested that—

(*a*) The size of chromosomes may be a specific diagnostic for species whose chromosomes are, otherwise, morphologically similar and equal in number. The measurements bring out a size difference in the chromosomes of the *Aloinæ*, which is particularly clear when the larger chromosomes of one species are compared with those of another species.

(*b*) Quantitative measurements of chromosome size should be used more generally as a method of verifying any speculations concerning the relation and origin of chromosome numbers in related species of plants.

(*c*) A comparison of the volume of chromatin in diploid and tetraploid species affords a clue to the origin of tetraploidy in the species concerned. In the tetraploid species of *Haworthia* the double number of chromosomes is the result of a duplication of the complete chromosome set of the nucleus. The volume of the chromatin at heterotypic metaphase in *Haworthia tesselata parva* is twice the volume of the chromatin in the nuclei of any of the allied species or genera examined during the investigation.

This research was carried out in the Botanical Laboratory of King's College, London, for the most part while the investigator was the recipient of a grant from the Department of Industrial and Scientific Research.

I wish to acknowledge my indebtedness to Prof. R. R. Gates, who, in the first place, suggested the chromosomes of the Liliaceæ as a subject for investigation, and I take this opportunity of expressing my gratitude for the interest he has shown in the research in all its stages.

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VIII.—EXPLANATION OF PLATES 18, 19.

All figures were drawn with a camera lucida under a $\frac{1}{12}$-inch apochr. hom. imm., Zeiss N.A., with comp. oc. 12 × 3,000.

Somatic Mitoses.

Fig. 1.—*Aloë abyssinica*. Somatic metaphase showing 14 chromosomes. Some of the chromosomes are already longitudinally split and all show to a greater or lesser extent the subterminal constriction.

Fig. 2.—*Aloë pluridens*. Somatic metaphase showing 14 chromosomes with subterminal constrictions. The constricted portion often doubled over at the point of constriction.

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Fig. 3.—*Aloë arborescens Natalensis.* Late prophase of a nucleus of the tapetal tissue (cut). Constrictions in two long chromosomes very clear and amount of constriction unequal.

Fig. 4.—Single chromosomes from dividing tapetal nuclei. Pronounced constriction at one end and second constriction shown at the other end. In chromosome A the main constriction occurs at a point much farther from the end than that in chromosome B.

Fig. 5.—*Gasteria Croucheri spathulata.* Profile view of spindle of a somatic division of the nucleus in anaphase. Note subterminal constrictions in all the chromosomes.

Fig. 6.—Part of one group of the anaphase of a somatic division showing the position of the constriction related to the spindle fibres. In one pair of long chromosomes the length of the constricted portion is about three times that of the constricted portion in the other chromosomes figured.

Fig. 7.—*Haworthia hybrida.* 8 long + 6 shorter chromosomes in metaphase of somatic division. Some of the large chromosomes show well-marked constrictions.

Fig. 8.—*Haworthia tesselata.* Metaphase of somatic division of a tetraploid species. Well-marked constrictions shown in all the chromosomes which lie in a favourable position.

Fig. 9.—*Apicra deltoidea.* Prophase of a somatic mitosis. The longitudinal halves are frequently much intertwined. The transverse constriction is very pronounced in some chromosomes. 14 chromosomes.

Meiosis.

Fig. 10.—*Aloë abyssinica.* Early diakinesis. Note the constrictions in some of the chromosomes.

Fig. 11.—*Aloë arborescens Natalensis.* 4 large + 3 small bivalents Note constriction in two of large bivalents. Two nucleoli [N].

Fig. 12.—Tangential section showing well-defined constrictions in large bivalent chromosomes.

Fig. 13.—*Aloë abyssinica.* Heterotypic metaphase. Polar view with 4 + 3 chromosomes going on spindle.

Fig. 14.—*Aloë arborescens Natalensis.* Heterotypic metaphase. Polar view with 4 + 3 chromosomes going on spindle.

Fig. 15.—*Gasteria retata.* Heterotypic metaphase. Polar view with 4 + 3 chromosomes going on spindle.

Fig. 16.—*Gasteria nigricans platyphylla.* Heterotypic metaphase. Polar view with 4 + 3 chromosomes going on spindle.

Fig. 17.—*Haworthia radula.* Heterotypic metaphase. Polar view with 4 + 3 chromosomes going on spindle. The univalent chromosomes of one small bivalent are already separating.

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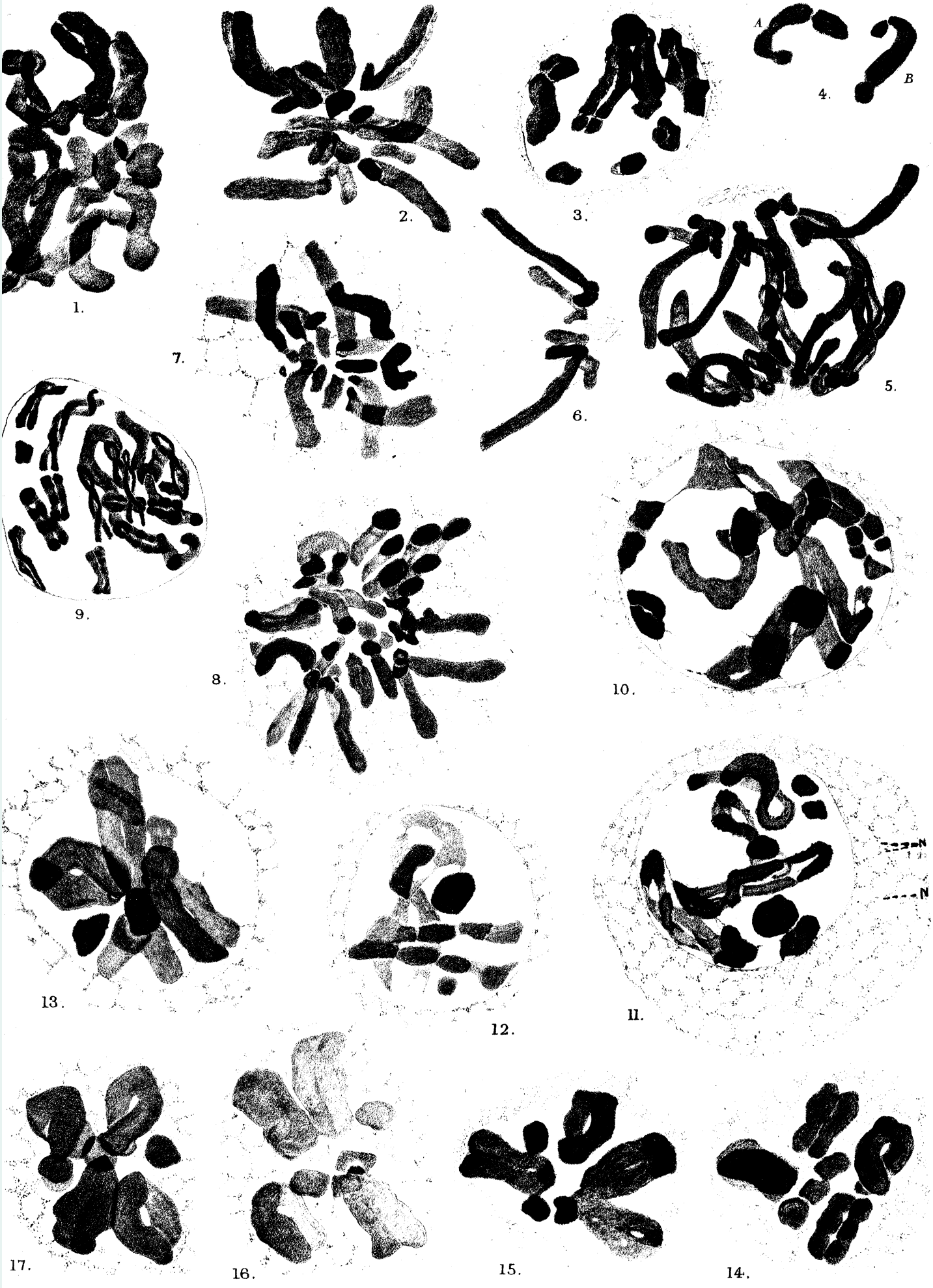

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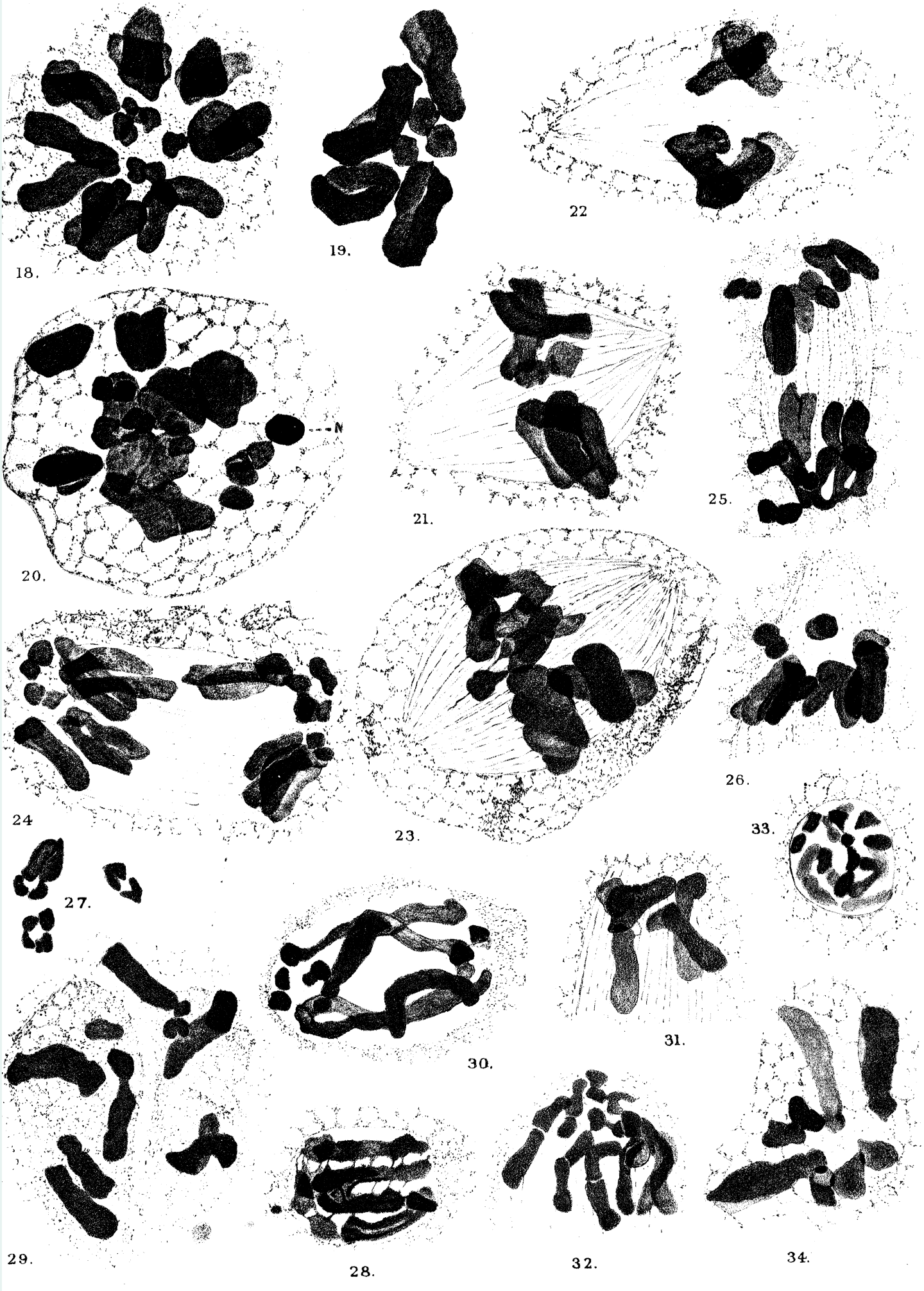

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Fig. 18.—*Haworthia tesselata parva.* Heterotypic metaphase, polar view showing 8 + 6 bivalent chromosomes of a tetraploid species.

Fig. 19.—*Apicra deltoidea.* Heterotypic metaphase.

Fig. 20.—*Apicra pentagona spiralis.* Chromosomes passing on to heterotypic spindle. Nucleolus present. Tetraploid species.

Fig. 21.—Section of heterotypic spindle in early anaphase. The large chromosome to right of figure showing the beginning of the homotypic split.

Fig. 22.—Section of heterotypic spindle showing only two chromosomes in early anaphase, with the homotypic split showing very clearly.

Fig. 23.—*Gasteria nigricans platyphylla.* Profile view of metaphase of first meiotic division. Note the attachment of the large chromosome on the left of the figure.

Fig. 24.—*Gasteria nigricans platyphylla.* Section of spindle at the anaphase of the first meiotic division, showing the split and constricted univalent chromosomes arriving at the poles.

Fig. 25.—*Aloë arborescens Natalensis.* Anaphase of first meiotic division, upper group cut, lower group showing 4 large + 3 small split and constricted univalent chromosomes.

Fig. 26.—One anaphase group of chromosomes only. Similar stage to that shown in Fig. 25. The small chromosomes travel first towards the poles.

Fig. 27.—*Aloë abyssinica.* Three chromosomes from a nucleus in early telophase. Note separation of the halves of the univalent chromosomes and very pronounced constrictions.

Fig. 28.—*Apicra deltoidea.* Telophase of first meiotic division. All the chromosome strands are not drawn. Nuclear membrane very faint on the side towards the spindle.

Fig. 29.—*Gasteria Holtzei.*—Homotypic chromosomes, some of which show the constrictions clearly.

Fig. 30.—One of the homotypic spindles, lower group of chromosomes cut. Constrictions clear in large chromosomes.

Fig. 31.—*Gasteria nigricans platyphylla.* Part of an anaphase group showing subterminal attachment of the spindle fibres.

Fig. 32.—*Gasteria nigricans crassifolia.* A part of an anaphase group of the homotypic division approaching pole of spindle. The chromosomes are constricted and again transversely segmented. Tetraploid species.

Fig. 33.—*Aloë abyssinica.* Homotypic telophase showing transverse segmentation of the chromosomes.

Fig. 34.—*Gasteria Cooperi.* Section of a metaphase of pollen grain nucleus seen obliquely. Note constrictions in the chromosomes.

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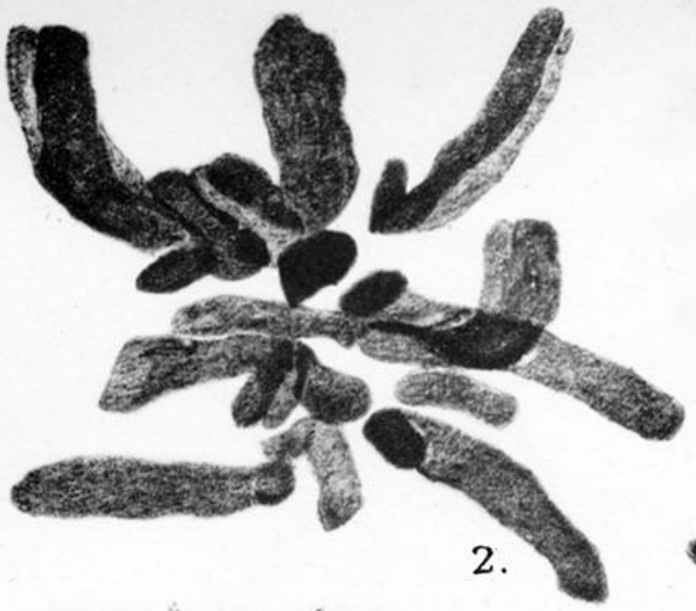

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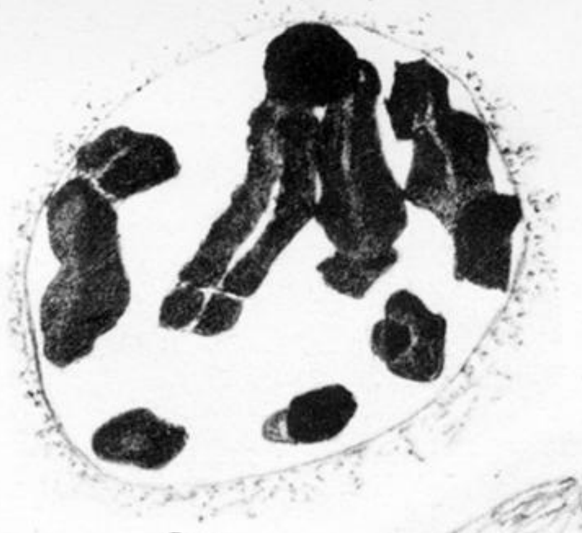

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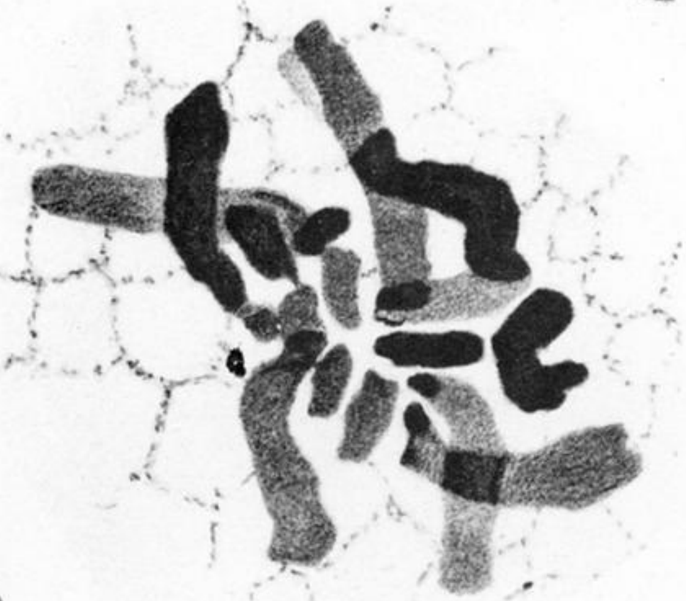

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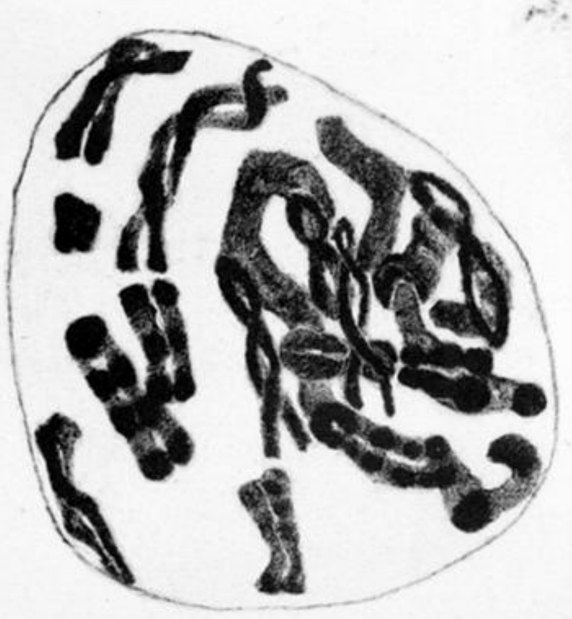

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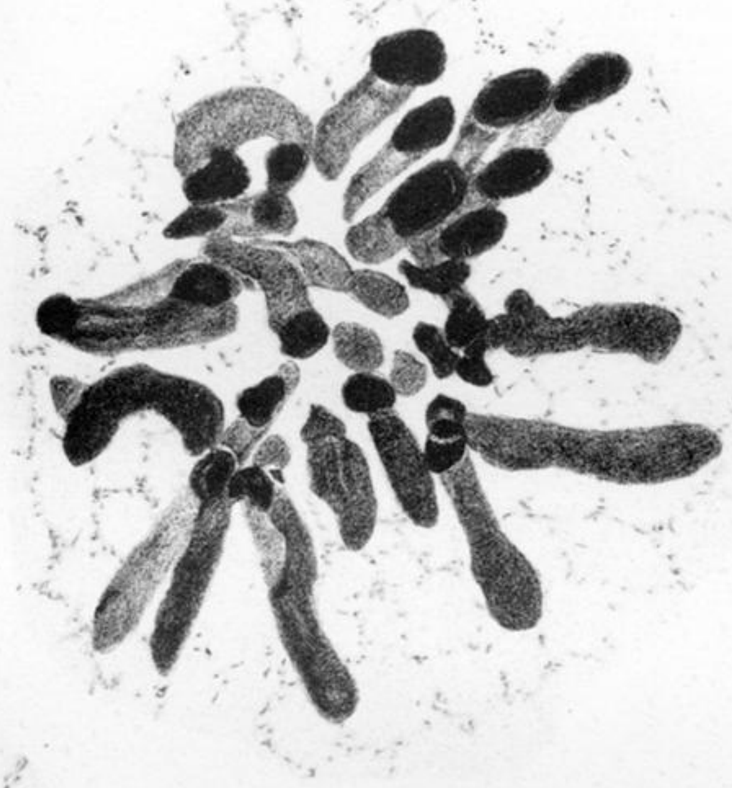

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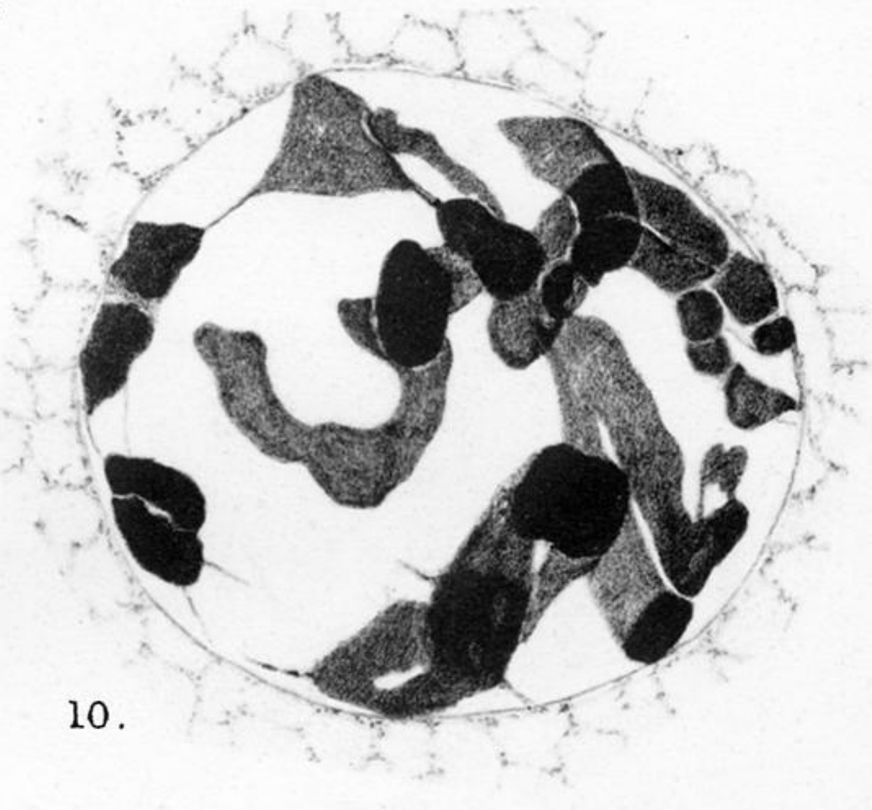

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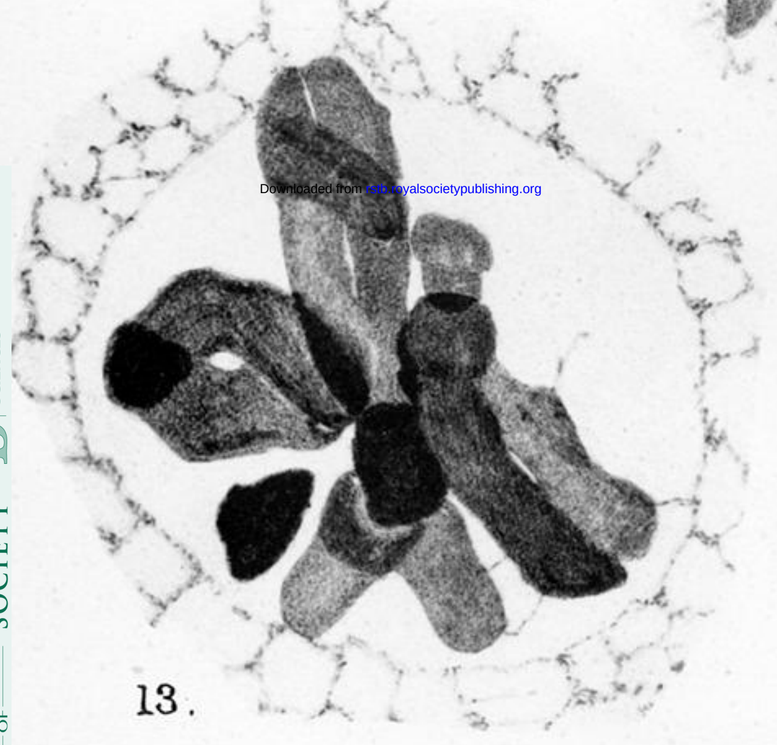

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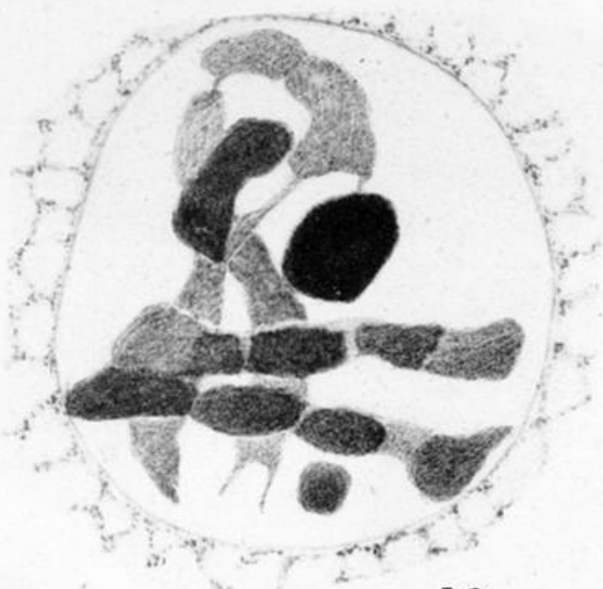

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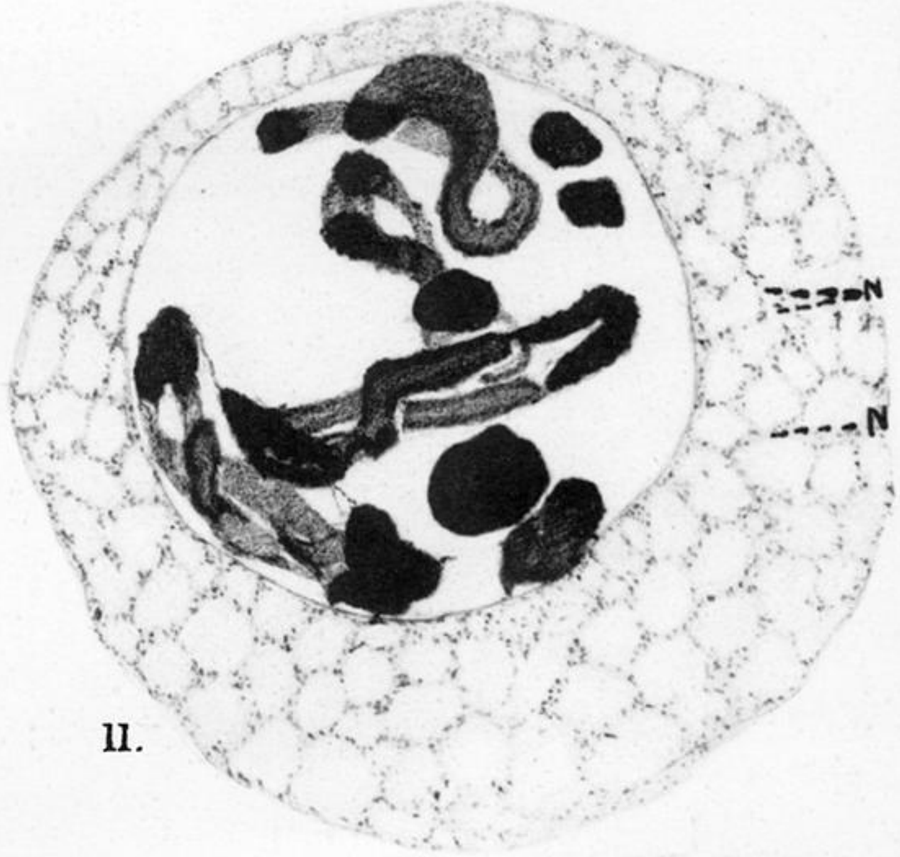

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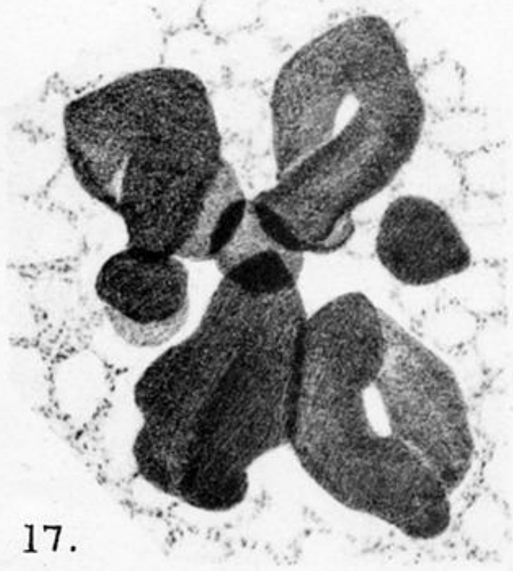

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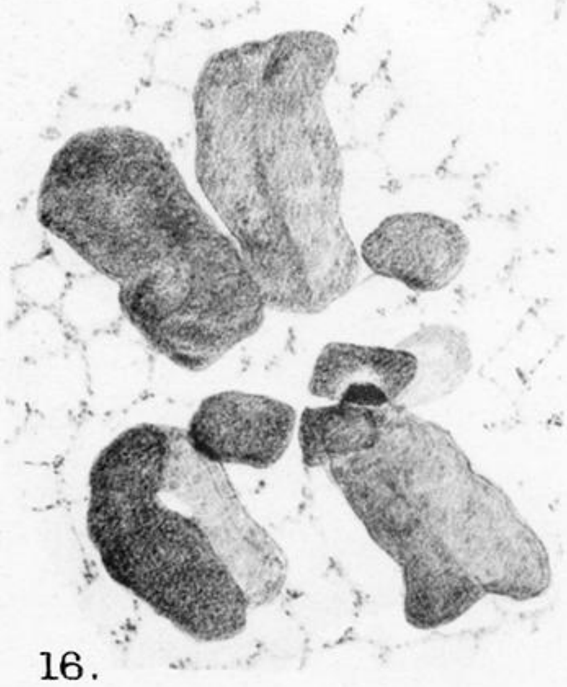

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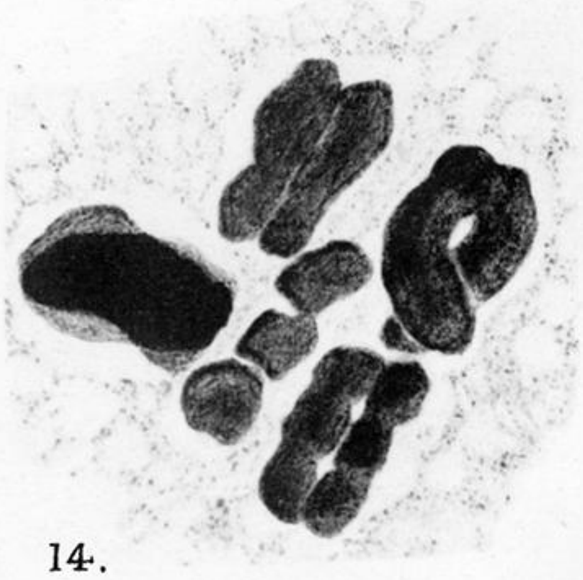

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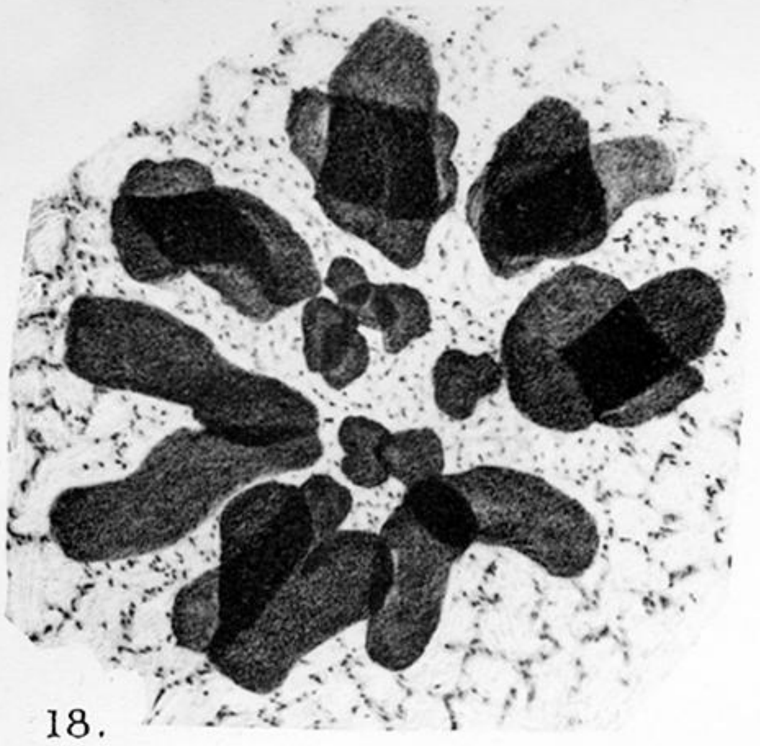

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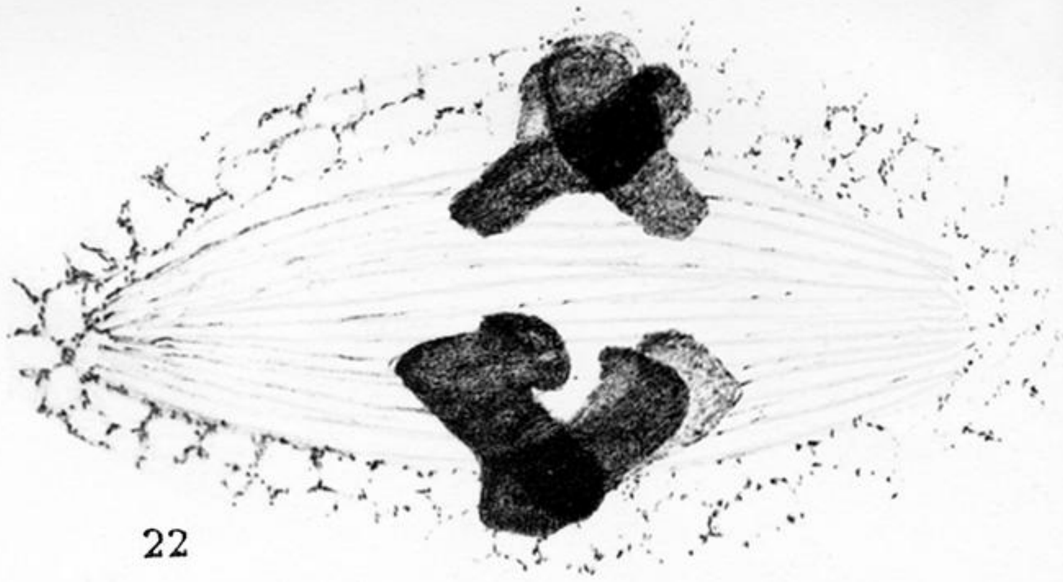

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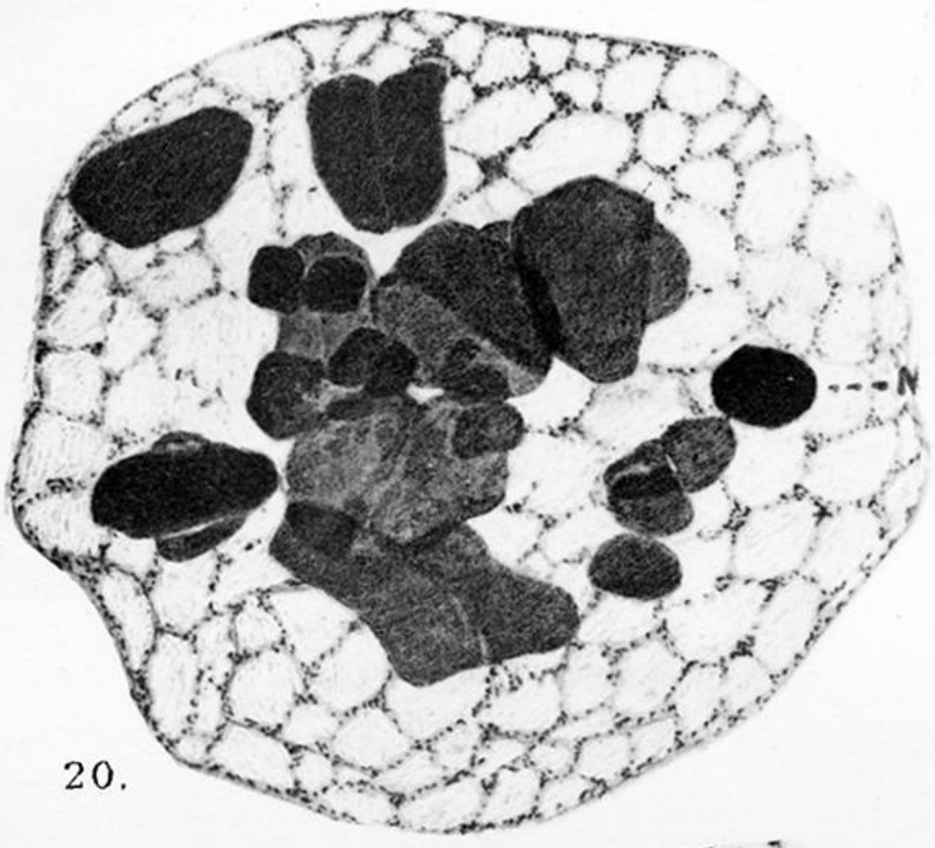

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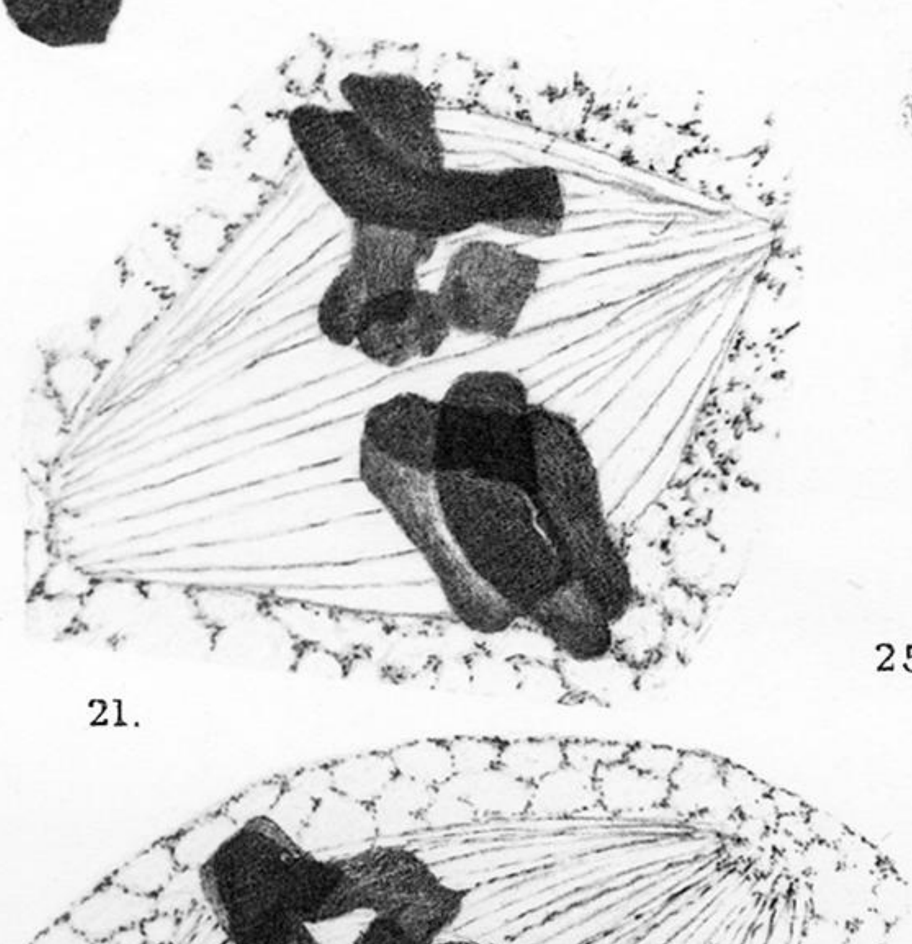

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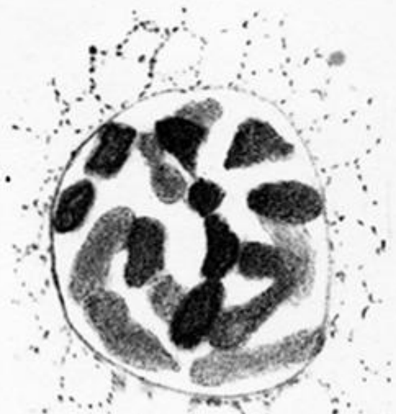

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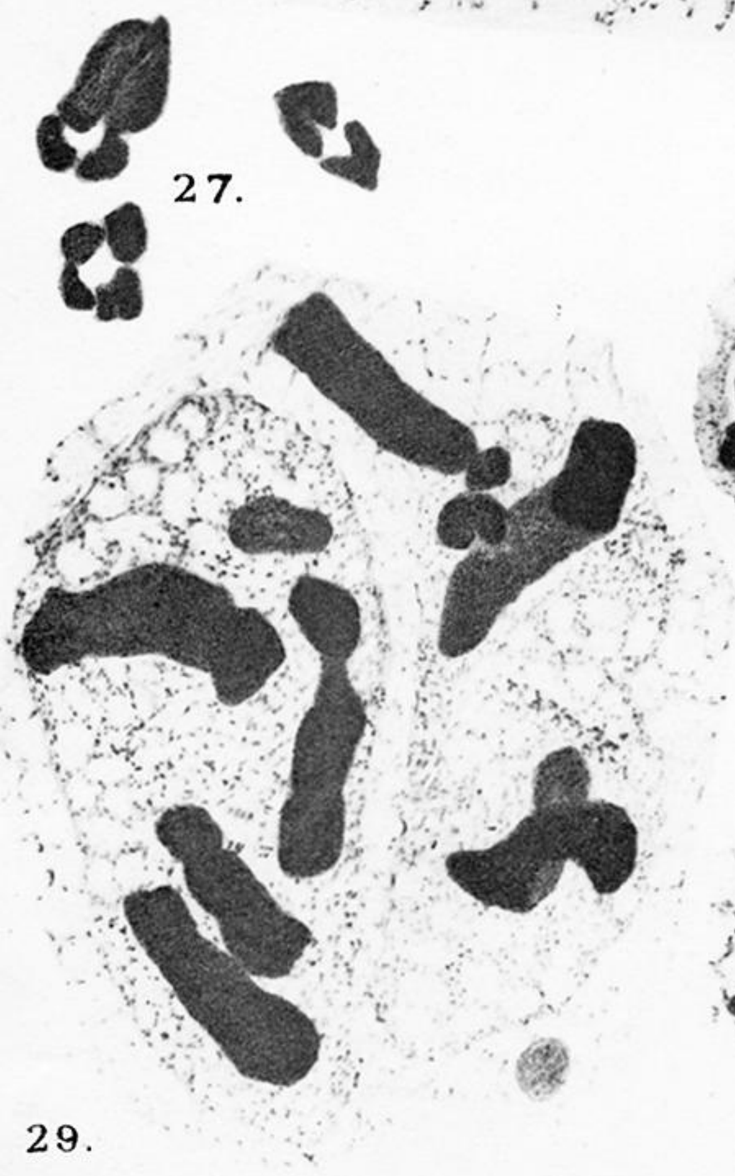

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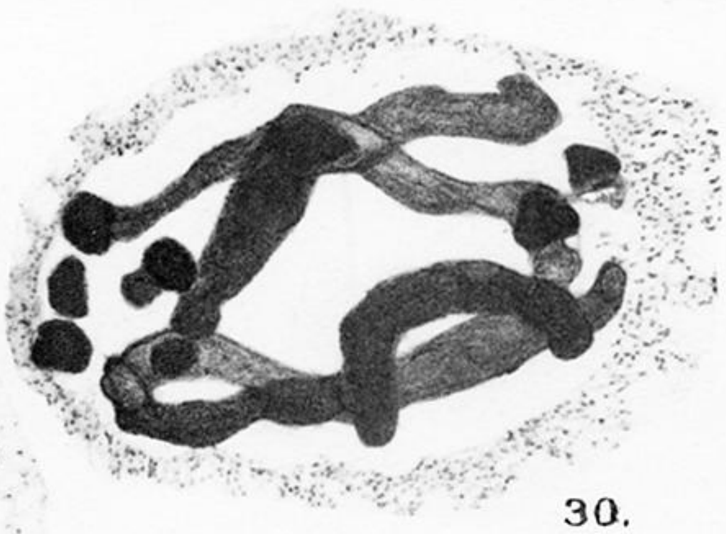

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