CYTOLOGY OF SOME SPECIES OF THE OPHIOGLOSSACEAE IN INDIA

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Abstract

Chromosome numbers in six species of *Ophioglossum* available in Poona and in *Helminthostachys zeylanica* L. obtained from Kerala are given. *O. nudicaule* L., *O. gramineum* Willd., *O. pedunculosum* Prantl (*sensu non*-Desv.) and *O. fibrosum* Schum. were found to have $n = 120$ chromosomes. *O. aitchisoni* d'Alm. had 210–215 bivalents, and *O. reticulatum* L. had $n = 420$. Of these the chromosome number in *O. peduculosum* was not reported before. Meiotic cycle in this species showed some irregularities such as bridge formation in some cases at anaphase I.

The paper further discusses the significance of polyploidy observed in *O. nudicaule* and traces the evolutionary trends seen in the genus on the basis of the chromosome numbers. There exists some sort of correlation between the size of plants and their chromosome numbers. No variation in the number of chromosomes in different plants of the same species growing in different localities was observed.

On the basis of the chromosomal analysis, it seems that *O. nudicaule*, *O. gramineum* group is more primitive and *O. aitchisoni*, *O. reticulatum* groups more advanced. This agrees with the conclusion drawn by one of us (Mahabalè, 1965) in this regard, on the basis of the morphology of species.

Introduction

The Ophioglossaceae form an interesting group of Eusporangiate ferns with several morphological as well as cytological peculiarities. It comprises three genera: *Ophioglossum* which is cosmopolitan having about 30 species, *Botrychium* with 12 species occurring mostly in mountainous regions, and

Helminthostachys having only one species. Cytology of these species has interested many botanists since long; some important workers dealing with it recently being Manton (1950, 1954), Abraham and Ninan (1954), Ninan (1956, 1958), Verma (1956), Abraham (1958), Kurita and Nishida (1965). The entire meiotic cycle in the members of this family was described long ago in *Botrychium virginianum* by Burlinghame (1907) and Steil (1935) and also in *O. vulgatum* by Steil (*loc. cit.*). Others have reported only the chromosome numbers. Recently Kurita and Nishida (1965) found that in *O. petiolatum* $n = 960$, 1,100, and in *O. thermale* var. *nipponicum* $n = 480$, 960 and also some irregularities in meiosis. Verma (1956) also reported $n = 400$ and more in *O. vulgatum*.

The present work deals with cytology in six species of *Ophioglossum* found in Poona undertaken with a view to finding whether the chromosome numbers in them varied from those already known in plants growing elsewhere.

MATERIAL AND METHODS

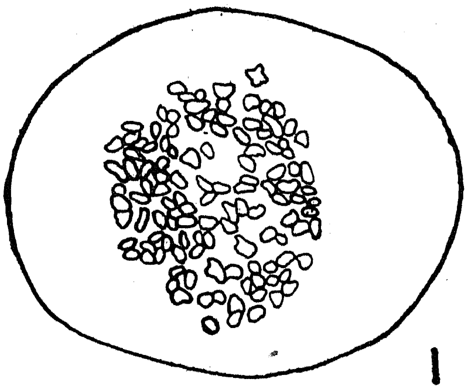
The species of *Ophioglossum* were collected in and around Poona and that of *Helminthostachys zeylanica* at Trivandrum. Squash preparations were made from the fresh material by usual acetocarmine technique. Microphotographs were taken using Perutz Panchromatic plates.

OBSERVATIONS

The chromosome numbers observed here in different species are given below:

(i) *O. gramineum* Willd.—The plants collected from the Poona University Campus showed $n = 120$ chromosomes at the first meiotic metaphase (Plate III, Fig. 1; Text-Fig. 1), also reported by Ninan (1958) for material from Palghat.

(ii) *O. nudicaule* L.—All the plants collected from the Poona University Campus showed $n = 120$ (Plate III, Fig. 2; Text-Fig. 2). In the material from Palai, Palghat and Kumbanad Ninan (1958) found $n = 240$. But in *O. nudicaule* var. *typicum* and *O. nudicaule* var. *tenerum* collected had $n = 120$ (Ninan, 1958). It seems that the two varieties of it growing at Bangalore and at Poona seem to agree in their cytology and morphology.



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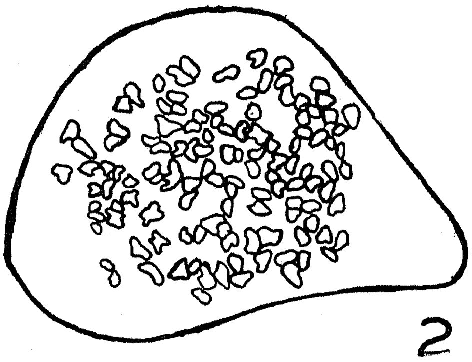

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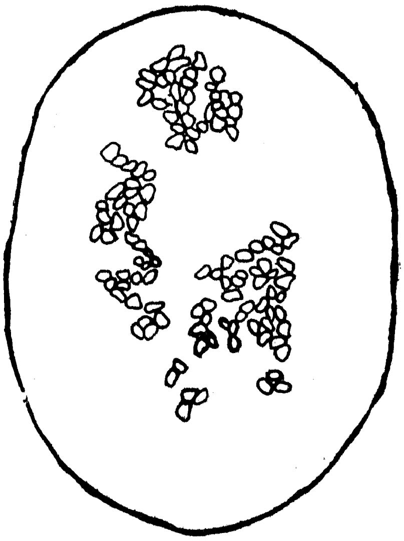

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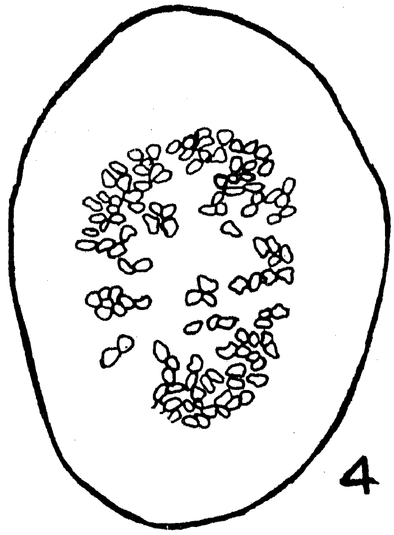

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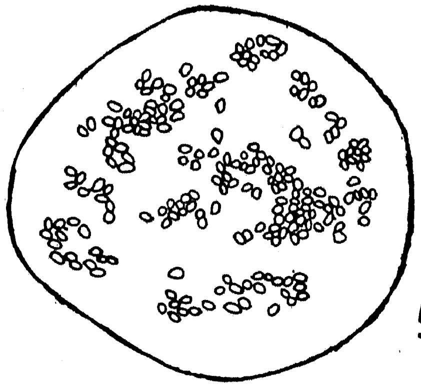

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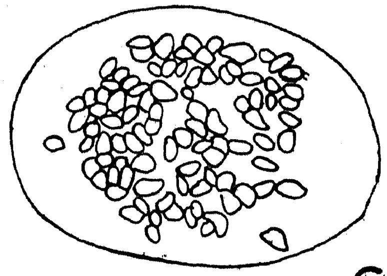

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TEXT-FIGS. 1–6. Chromosome numbers in *Ophioglossum* species and *Helminthostachys zeylanica* L. Fig. 1. *O. gramineam* Willd. showing 120 bivalents at first meotic metaphase, × 430. Fig. 2. *O. nudicaule* L. metaphase plate with 120 bivalents, × 430. Fig. 3. *O. pedunculosum* Prantl (*sensu non*-Desv.) Metaphase plate showing 120 bivalents, × 430. Fig. 4. *O. fibrosum* Schum. 120 bivalents af first meiotic metaphase, × 430. Fig. 5. *O. Aitchisoni* d'Ahm. showing 215 bivalents at first meiotic diakinesis, × 430. Fig. 6. *Helminthostachys zeylanica* L. showing 94 bivalents at first meiotic metaphase, × 430.

(iii) *O. fibrosum* Schum.—Plants were collected at Khandala. Here the spore mother cells had 120 bivalents (Plate III, Fig. 3; Text-Fig. 3) which agrees with the number reported by Ninan (1956) for plants from Palghat.

(iv) *O. pedunculosum* Prantl (*sensu non*-Desv.). The chromosome number in this species was not reported before and hence it was worked out in detail. The spore mother cells in this plant showed 120 bivalents at I meiotic metaphase (Plate III, Fig. 4; Text-Fig. 4).

The meiotic cycle in this species is similar to that in other species, but it did show some abnormalities (Plate III, Figs. 7–18). Meiotic divisions in the spore mother cells in sporangia on a spike start basipetally and extend towards the apex. The primary spore mother cells divide rapidly and fill the sporangial cavity and soon get separated into assorted blocks before they undergo meiotic cycle. They are thin-walled and have large oval or round central nucleus. During early prophase the nuclear membrane enlarges and the nucleolus becomes prominent (Plate III, Fig. 7). Karyolymph becomes hyaline and the chromatin network is seen as a mass of loosely entangled threads. The chromosomes could be distinguished as distinct entities from the pachytene stage onwards. During diakinesis most of the bivalents were free from chiasmata, but some did show X, O and rod-shaped configurations (Plate III, Figs. 8 and 9). The bivalents were more or less evenly distributed throughout the karyolymph. Nuclear membrane disappeared at the late prophase though the nucleolus was present. In some spore mother cells there were two nucleoli. Ring-like configuration of the chromosomes was also seen (Plate III, Figs. 8 and 10). Some of the spore mother cells had two or three nucleoli (Plate III, Fig. 11). As the metaphase proceeded, chromosomes got condensed and arranged themselves on the equatorial plate. Multivalents were not generally observed. At anaphase most of the spore mother cells showed normal separation into two groups (Plate III, Fig. 12), but in some the bridge formation was seen in about 1% of the cells (Plate III, Fig. 13). Telophase was normal (Plate III, Figs. 14 and 15). No wall was formed in the spore mother cells after the first division (Plate III, Fig. 15). The second division was normal (Plate III, Figs. 16–18). The wall formation took place by simultaneous furrowing (Plate III, Fig. 18). Isobilateral tetrads were usual. Tetrahedral or linear tetrads were also seen rarely.

(v) *O. aitchisoni* d'Alm. (*O. polyphyllum* R. Br.).—The specimens of this species at Poona showed $n = 210–215$ at the first meiotic metaphase and diakinesis (Plate III, Fig. 5; Text Fig. 6). This number does not agree either with $n = 116$–117 reported by Verma (1956–57) or $n = 120$ given by Ninan (1958), despite the fact that Ninan's material was also from Poona.

(vi) *O. reticulatum* L.—Plants of this species growing at Purandhar showed 420 bivalents at the first meiotic division (Plate III, Fig. 6). The chromosome number was mainly counted from diakinesis. Earlier Abraham and Ninan (1954), and Ninan (1958) have reported much larger n-number than this (*see* Table I). The number $n = 420$ found here is the lowest so far reported for this species.

(vii) *Helminthostachys zeylanica* L.—The material of this species collected at Trivandrum showed $n = 94$ in the primary spore mother cells. This number is the same as was reported by Ninan (1958) for this species (Text-Fig. 6).

DISCUSSION

(1) n-*Number of chromosomes*.—Out of the six species of *Ophioglossum* studied here, four have shown the same chromosome number, $n = 120$, whereas the remaining two showed higher numbers. On the basis of n-number of chromosomes, the species worked out can be divided into three groups:

Group I.—In this the lowest number of chromosomes is found, *viz.*, $n = 120$; *e.g.*, *O. gramineum*, *O. nudicaule*, *O. pedunculosum*, *O. fibrosum*.

Group II.—This has a higher chromosome number, $n = 210$–215 observed in a single species, *O. aitchisoni*.

Group III.—In this group $n = 420$ as in *O. reticulatum*. Of these three groups, Group I—*O. gramineum*, *O. nudicaule* seem to be very primitive and Group III the most advanced. This agrees with the conclusions drawn by one of us on the basis of their morphology, leaf venation and anatomy (Mahabalé, 1962).

(2) *Basic number*.—Since the chromosome numbers in *Ophioglossum* species are varied, $n = 120$, 210–215, and 420, there might have been duplications on account of which they are forming a polyploid series with basic chromosome number assumed to be 15, as all known numbers are multiples of 15. Alternatively they might have been derived from different basic numbers. However, it should be remembered, as rightly pointed out by Manton (1950), that here we are dealing only with the end products of a

TABLE I

Showing the chromosome numbers in species Ophioglossaceae so far reported by the various authors

Species*	Locality	Chromosome No. (*n*)	Author	Year
Ophioglossum vulgatum L.	.. Europe	250	Sorsa	1962
do.	.. England	250–260	Manton	1950
do.	.. Darjeeling (N. India)	480	Verma	1956
do.	.. Amritsar	340–346	do.	1956
do.	.. Amritsar	385–390	do.	1956
do.	.. Mussoorie	410–420	do.	1956
do.	.. Amritsar	410	do.	1956
do.	.. Amritsar	465–475	do.	1956
do.	.. Amritsar	515–520	do.	1956
do.	.. Europe	240	do.	1958
do.	.. Europe	247–251	do.	1958
do.	.. Munnar (S.India)	570	Ninan	1958
do.	.. India	150–160 Ca. 300	Roy and Pandey	1963
do.	.. Europe	344	Ebrenberg	1945
do.	.. Japan	240	Kurita and Nishida	1965
do.	.. India	Meiosis irregular, over 400	Verma	1956

s.s.p. *ambigium* var. *islandicum*	Europe	480	Love and Love	1961
O. reticulatum	Trivandrum City	564	Abraham and Ninan	1954
do.	Sea Coast	2nd pl., 1972		
do.	Parambikulam (S.-India)	566	do.	1954
do.	200 Miles N. of Trivandrum City	2nd pl. 631	..	..
do.	Ponmudi (S. India) (40 miles N.E. of Trivandrum)	451	do.	1954
do.	Ettapadappu (12 miles N.E. of Ponmudi)	436	do.	1954
do.	Bonaccord Estate near Ponmudi	480	do.	1958
do.	Trivandrum City	495	Ninan	1958
do.	Trivandumr City	570	do.	1958
do.	Mysore, Trichinopoly, Bengal & Dehra Dun	570	do.	1958
do.	Purandhar (Poona)	420	Mahabalë and Nair	..
O. petiolatum	Ettapadappu (S. India)	480	Ninan	1958
do.	Ceylon	Ca. 510	Manton and Sledge	1954
do.	Rajasansi (Amritsar)	510–515	Verma	1956
do.	Japan	510–520	Kurita and Nishida	1965
do.	Japan	480	do.	1965
do.	Japan	Meiosis irregular prob. 1100	do.	1965
do.	Japan	Meiosis irregular prob. 960	do.	1965

TABLE I—*Contd.*

Species	Locality	Chromosome No. (*n*)	Author	Year
O. ellipticum (= *O. petiolatum*)	Japan	Ca. 172	Yuasa	1934
O. aitchisoni	Poona	120	Ninan	1958
do.	Poona	210–215	Mahabalé and Nair	..
O. polyphyllum (= *O. aitchisoni*)	Hoshiarpur	116 or 117, 120	Verma	1956
O. fibrosum (= *O. costatum*)	Palghat (S. India)	Over 190	Maheshwari and Singh	1943
O. costatum	Palghat (S. India)	120	Ninan	1956
do.	Africa	Ca. 116	Manton	1956
O. fibrosum	Belgaum	120	Ninan	1958
do.	Khandala	120	Mahabalé and Nair	..
O. gramineum	Palghat (S. India)	120	Ninan	1958
do.	Poona	120	Mahabalé and Nair	..
O. lusitanicum	England	123–130	Manton	1950
do.	Thambaram, Belgaum, Veli, Palghat, Palai Kumbanad (India)	240	Ninan	1958
ssp. *coreaceum*	Australia	510	Verma	1956
O. nudicaule	India	240	Ninan	1956–58
do.	Poona	120	Mahabalé and Nair	..
O. nudicaule var. *typicum*	Bangalore	120	Ninan	1958
do. var. *tenerum*	Bangalore	120	Ninan	1958

O. pendulum ..	Ceylon	Ca. 370	Manton	1953
do. ..	Ceylon	Ca. 480	Ninan	1958
O. coreaceum ..	New Zealand	Ca. 360	Brownlie	1953
O. thermale var. *nipponicum* ..	Japan	240	Verma	1957
do. ..	Japan	480	Kurita and Nishida	1965
do. ..	Japan	Meiosis irregular prob. 960	do.	1965
O. pendulum var. *typicum* ..	Ceylon	370–380	Manton and Sledge	1954
O. pedunculosum Prantl *sensu non*-Desv.	Poona	120	Mahabalé and Nair	..
O. pendulum var. *typicum* ..	Ceylon	Ca. 480	Ninan	1958
O. gramineum ..	Palghat	120	do.	1958
Helminthostachys zeylanica ..	Trivandrum	94	do.	1958
do. ..	Trivandrum	94	Mahabalé and Nair	..

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* Modified from Kurita and Nishida (1965).

discontinuous series existing today. The basal number in them and their intermediates we do not know. Possibly they have been lost in antiquity.

(3) *Size of chromosomes.*—The size of the chromosomes in *Ophioglossum* is variable. It varies from $2 \cdot 5\,\mu$ to $4 \cdot 5\,\mu$. With increase in the number of chromosomes there is a decrease in their size as in *Luzula*, etc. Thus in *O. reticulatum* belonging to Group III there are 420 bivalents, but the chromosomes are comparatively smaller, $2 \cdot 5\,\mu$, compared with those in *O. fibrosum*, *O. nudicaule*, *O. pedunculosum* and *O. gramineum* in which $n = 120$, and the size of chromosomes is $4 \cdot 3\,\mu$. In *O. aitchisoni* with $n = 210$–215, the chromosomes are medium-sized, $3 \cdot 5\,\mu$. According to Manton (1956) with the passage of time nuclear or physiological readjustment must have occurred for the restoration of plants to sustain repeated polyploidy on such a large scale which would otherwise have made the continuance of these plants impossible. The diminution in size of chromosomes might perhaps be one of such adjustments. According to her, when polyploidy is extensively operating, as in *Ophioglossum*, it is likely that the plants with lower number of chromosomes might have gone out of existence first in course of time, leaving plants with higher chromosome number to continue and survive. It should also be remembered that in this genus the population is mixed, some plants having been derived from vegetative buds and a few from prothalli.

Simultaneously with the diminution in size of chromosomes and increase in their number, there is enlargement in the size of the spore mother cells. The largest size of spore mother cells among the six species studied is $118 \cdot 3\,\mu \times 112\,\mu$ in *O. reticulatum*. In other species it varies from $48\,\mu \times 38\,\mu$ to $118\,\mu \times 112\,\mu$.

There is some relation between the size of plants in different species and their chromosome numbers. But Kurita and Nishida (1965) do not agree with this view. For example, in Group I plants have $n = 120$ in *O. pedumculosum*, *O. nudicaule*, *O. fibrosum* and *O. gramineum*. These plants are small, 2–4·5 cm high compared with those in *O. reticulatum* belonging to Group III having a height 12–16 cm and chromosomes $n = 420$. *O. Aitchisoni* with $n = 210$–215 has medium-sized plants, 8–11·5 cm high. Presumably this is also true of *O. vulgatum* belonging to the same group. It has 240–540 chromosomes and plants vary in size from 12–20 cm. in height.

A survey of the chromosome numbers in the seed plants shows that higher chromosome numbers have been evolved from the lower ones by polyploidy. The same process must have been operating in the lower vascular plants also. However, as none of the living species of *Ophioglossum* show a number lower than 120, direct establishment of a real basic number or numbers is not possible. Abraham and Ninan (1954) have reported the occurrence of over 500 diploid chromosomes in *O. reticulatum* from Parambikulam in South India. Probably auto- or allo-polyploidy or a combination of both might have taken place in this genus at some stage or the other in the course of its long history as suggested by Mehra (1961). In the absence of any multivalents in the material of the species we studied, it is rather difficult to conclude emphatically, but there could be little doubt that duplication of chromosomes has taken place in the evolution of species of this genus.

However, some disadvantages do arise from such repeated duplication and multiplication of chromosomes. Firstly, the plants tend to propagate vegetatively more and more, and the sexual phase gets practically suppressed, resulting in mixed population. It has also developed mycotrophic habit by way of adaptation at some stage as Mahabale (1969) suggests. Vegetative reproduction seems to have become dominant since it is the chief mode of their propagation. Genomic variation, aneuploidy, autopolyploidy and allopolyploidy, geophilous habit, mycotrophic association all seem to have played their part in the evolution of this genus, on account of which it shows a variety of chromosome numbers.

In this connection the multivalent associations reported by Verma (1956) in *O. vulgatum* are noteworthy. Manton (1954), Abraham and Ninan (1954), and Ninan (1956, 1958) did not observe any such multivalents in their material. In the present investigation also no multivalents were seen, although polyploidy was evident in *O. nudicaule*. It is well known that polyploid species have a tendency to form multivalents associations. However, in our material only bivalents were observed in all the cases irrespective of their n-number = 120, 210–215 or 420. The only explanation of these anomalous facts would be that both autopolyploidy and allopolyploidy might have been working in their evolution, rather in quick succession.

Another point observed by Verma (1956) in *O. vulgatum* is the intraspecific genomic variability. He not only observed different chromosome numbers in *O. vulgatum* collected from different localities in Punjab, but also found varying n-numbers in different plants collected from the same locality near Amritsar, *viz.*, 240, 385–390, 410, 515–520. Kurita and Nishida (1965) reported 240 bivalents in *O. vulgatum* for the Japanese material they studied. Manton (1960) found 250–260 bivalents in the specimens of the same species collected in England. According to Verma (1956) there is a definite correlation between the chromosome numbers and the size of the plants, although Kurita and Nishida (1965) do not think that there is such a correlation. Our studies do seem to support Verma (1956) on this point. For example, in *O. nudicaule* Ninan (1958) observed $n = 240$ in the larger specimens occurring at Belgaum, Veli, Pali, Palghat and Kumbanad, whereas in the two smaller varieties of the same species, *viz.*, *O. nudicaule* var. *tenerum* and *O. nudicaule* var. *typicum* growing at Bangalore, Poona and Khandala there were 120 bivalents and the plants of these were small, 1–2·5 cm. Possibly within the same species there seems to exist a secondary polyploid series giving rise to different varieties and races. In *O. reticulatum* also Abraham and Ninan (1954) found different chromosome numbers in different plants growing in the same locality (*see* Table I), and also different chromosome numbers in plants growing in different localities. For example, in plants of *O. reticulatum* collected at Parambikulam there were 566–631 bivalents. In our plants collected at Purandhar n-number was different, $n = 420$. This is the lowest number so far reported for this species. In *O. lusitanicum* from Guernsey, Manton (1956) has reported $n = 125$–130, whereas Ninan (1956 *a*) reports $n = 240$ for Thambaram specimens. In *O. pendulum* from Ceylon Manton (1956) reports $n = 370$ and Ninan (1956) $n = 480$ for the material of the same species obtained from Ceylon. Evidently there is variation in the chromosome numbers in the plants of the same species growing in the same area, or that the n-number may remain the same, possibly in a clonal group. Such variations are generally correlated with their geographical distribution and speciation. *O. nudicaule* worked out in the present investigation illustrates this point well. In the specimens of this plant growing in the extreme South India, the n-number was 240, whereas in the specimens of the same species collected at Poona it was 120. The same thing is true of the plants of *O. lusitanicum*, *O. reticulatum* and *O. vulgatum* growing at different places and localities in India.

In specimens of *O. reticulatum* collected at Parambikulam itself a difference of 65 bivalents has been reported by Abraham and Ninan (1954). Even then, this inordinate increase in the chromosome number by 65 does not seem to cause any noticeable change in the broad external morphology of the plants. Verma (1956) found still greater difference of 180 bivalents in the plants of *O. vulgatum* collected at different places in Amritsar alone. One wonders, how in spite of these additional chromosomes, there is not much significant change in the external morphlogy of the plants; or is it that they carry some inert genes or B chromosomes ? It is impossible to give a difinite answer to this question due to very small size of chromosomes and very large numbers. One will have to investigate several populations for that purpose from different places

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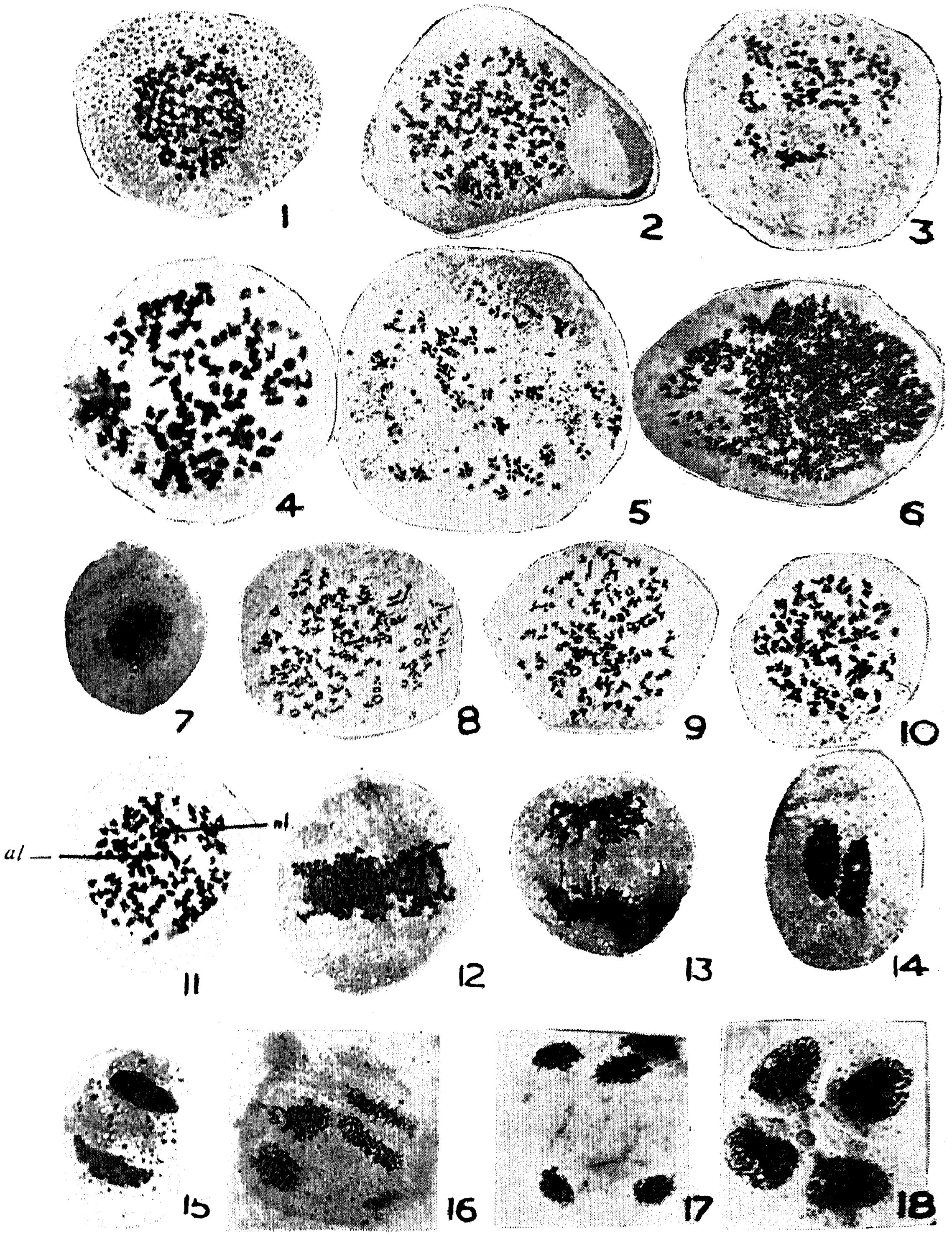
EXPLANATION OF PLATE III

FIGS. 1–18. Figs. 1–6. Chromosomes in species of *Ophioglossum*. Fig. 1. *O. gramineum* Willd. Metaphase plate showing 120 bivalents, × 269. Fig. 2. *O. mudicaule* L. Metaphase plate showing 120 bivalents, × 297. Fig. 3. *O. fibrosum* Schum. Metaphase plate showing 120 bivalents, × 292. Fig. 4. *O. pedunculosum* Prantl. (*sensu non*-Desv.). Metaphase plate showing 120 bivalents, × 292. Fig, 5. *O. aitchisoni* d'Alm. Diakinesis showing 215 bivalents, × 282. Fig. 6. *O. reticulatum* L. Diakinesis showing 410 bivalents, × 322. Figs. 7–18. *O. pedunculosum* Prantl (*sensu non*-Desv.). Fig. 7. Prophase, × 291. Fig. 8. Early diakinesis—note X, O and rod-like configurations, × 261. Fig. 9. Late diakinesis, × 268. Fig. 10. Early metaphase, × 268. Fig. 11. Metaphase—note two nucleoli—*nl*, × 292. Fig. 12. Early anaphase × 288. Fig. 13. Anaphase—note the chromatid bridge, × 256. Fig. 14. Telophase I, × 293. Fig. 15. Late telophase I, × 243. Fig. 16. Early telophase II, × 226. Fig. 17. Late telophase II, × 280. Fig. 18. Isobilateral tetrad, × 260.



FIGS. 1–18