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## SOME ASPECTS OF THE LIFE HISTORY AND CYTOLOGY OF *STICTYOSIPHON TORTILIS* (RUPR.) REINKE

NEKI ASPEKTI RAZVITKA I CITOLOGIJE VRSTE STICTYOSIPHON TORTILIS (RUPR.) REINKE

M. Naylor



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### SOME ASPECTS OF THE LIFE HISTORY AND CYTOLOGY OF *STICTYOSIPHON TORTILIS* (RUPR.) REINKE

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Margaret Naylor University of Hull Submitted at the Symposium of Algologists, July 1957 Institute of Oceanography and Fisheries, Split, Yugoslavia

#### ABSTRACT.

Swarmers from the macroscopic plants of *Stictyosiphon tortilis* gave rise to creeping, filamentous germlings reproducing by plurilocular sporangia and persisting for several months. Chromosome counts of 26 have been obtained for the germlings and in the developing sporangia. Several counts of more than 40 chromosomes have been made on the vegetative cells of the macroscopic plant, but no sufficiently well spread metaphase plates have been found to give an accurate count.

#### OCCURRENCE ON THE SHORE.

Plants of *Stictyosiphon tortilis* (R u p r.) Reinke are seasonal in their occurrence on the shore. On the Yorkshire coast, at Scarborough and at Filey, vegetative growth commences early in the year and by March to April the plants form small clumps about 5 cms. high. Rapid growth follows and large, freely branched plants about 30 cms. high are formed (Plate I). Throughout the Summer months these plants produce a succession of sporangia and then die back in the Autumn. A few sporangia may be found on the plants as early as January, but no appreciable liberation of the swarmers takes place until May. The fate of these swarmers could not be followed on the shore since the plants have only been found growing in pools with sandy bottoms.

The entire plant does not always die back in the Autumn: the attaching disc and the basal regions of the axis sometimes persist during the Winter and proliferate to give new growth in the following Spring. The plants found on the shore very early in the season appeared to have overwintered in this fashion, whilst those appearing later seemed to be entierely new growths.

In order to follow the life history of the plant, swarmers released from the sporangia were grown in culture using methods already employed in other species (Naylor, 1954). Cytological preparations were made both of the germlings and of the macroscopic plants.

#### CYTOLOGICAL TECHNIQUES.

#### I. MACROSCOPIC PLANTS.

The plants collected from the shore and those grown in culture were treated in the same way. Fixation was either with Karpechenko Fluid or with 3 parts absolute alcohol to 1 part glacial acetic acid. After 18 - 24hrs. fixation the material was washed and transferred for 4 hrs. to 30 per cent hydrogen peroxide. Storage was in a freshly made solution of 3 parts of absolute alcohol to 1 part of glacial acetic acid with a few drops of ferric acetate solution added, and staining was with acetocarmine. Before staining, the excess storage fluid was removed by washing to prevent blackening, and the portion to be stained warmed in a drop of 6 per cent Na<sub>2</sub> CO<sub>3</sub> solution. This softens the cell walls and the preparation can be thoroughly squashed, irrigated with water and then stained with acetocarmine.

#### II. GERMLINGS.

Al the plants used in this investigation were grown in culture during June and July, 1956. Plants of 7 and 8 days old were found to contain abundant nuclear divisions.

The most satisfactory results were obtained if the plants to be fixed were placed in the refrigerator overnight and then for two hours at room temperature under a bright light. After this treatment numerous cells at all stages of division could always be found. In some cases the plants were placed in a 0.1 per cent solution of colchicine for the two hours before fixation, but this did not appear to affect the results appreciably.

Fixation was in 3 parts absolute alcohol to 1 part glacial acetic and this was followed by staining with acetocarmine. Clear differentiation of the chromosomes was obtained, but the treatment did not soften the cell walls sufficiently for the chromosomes to become well spread. Possibly the treatment with  $H_2O_2$  and  $Na_2CO_3$  adopted for the macroscopic phases might remedy this defect.

#### Nc. 16

#### III. THE CHROMOSOME COUNTS.

Because of the small size of the chromosomes, counts could only be made by the employement of photographic tecniques. The figures were photographed in as many optical planes as possible and to the greatest magnification that could be obtained. Enlargements were then made to 8,000 diameters, the chromosomes outlined with indian ink, the prints bleached and superimposed and the resulting figure checked visually against the nucleus.

#### DEVELOPMENTAL MORPHOLOGY.

The swarmers, as described by K u c k u c k (1912), are pyriform with a single plastid and a crescentic eye-spot, and they swim actively for up to about half an hour before settling on the bottom of the container: the period of activity can be extended by placing the swarmers in a bright light and repeatedly stirring the solution. They show no marked phototactic response.

Within two hours of their release from the sporangia, the swarmers round off and become attached so firmly to the slides provided that they can not be dislodged with a jet of water. In the material examined no trace of fusion between swarmers was seen, nor any instances of »clumping« or »adelphtotaxis« as is seen in *Scytosiphon lomentaria* (S a u v ag e a u, 1929: p. 332). Only a single eye-spot was ever observed in the embryospores which were about 6  $\mu$  in diameter. K u c k u c k (1912), however, reported fusion between swarmers with the formation of zygospores with two eyespots. He stated further that the plants were always moneocius, and the swarmers positively phototactic.

Germination commences immediately and in 24 hours the majority of the germlings are two celled. Germination is iniciated by a germ tube, orientated at random with respect to the direction of indident light (Text figure 1 A). Possibly there may be a correlation between the random orientation of the germ tube and the lack of any phototactic response in the swarmers (N a y l o r, 1956b). The eye-spot sometimes reamins in the embryospore, sometimes it passes into the germ tube. Further divisions follow rapidly, producing at first a uniseriate, later a richly-branched, filament. The rounded embryospore remains evident at one end of the filament whilst growth in length takes place largely by the activity of



Text figure 1. a. Group of germinating spores 24 hrs. old showing the random orientation of the germ tubes. In some the eyespot (st) has passed into the germ tube, in other it has remained in the spore.

b. Germling 48 hrs. old with eyespots (st) still visible. The line in the centre represents a length of 20  $\mu.$ 

an elongated apical cell, with intercalary divisions resulting in branching (Text figure 2). The eye-spot persists for a day or two and then disappears.

At first the filaments were closely adherent to the substrate and composed of barrel-shaped cells each containing a single, parietal plastid R o s e n v i n g e (1935, p. 8) described the cells as containing several disc-shaped plastids, but in the plants examined such discoid plastids were only seen occasionally in some of the later formed cells. A similar occurrence of germlings with a single, saddle-shaped plastid in each cell whilst the macroscopic plant possesses several discoid plastids in each cell has also been observed by the author in *Striaria attenuata*. Staining with Heidenhain's haematoxylin shows that each cell contains about 6 pyrenoids.

In 6 - 10 weeks the germlings grew into hemispherical cushions 1 - 2 mm. in diameter composed of branched and radiating filaments. The terminal portions of some of the branches developed into sporangia, remaining for the most part uniseriate, but with a few longitudinal walls (Text figure 3 a, b). Each compartment gave rise to a single swarmer with one plastid and a conspicuous eyespot.

These fertile portions closely resemble in form those figured by K y lin (1933) in *Litosiphon pusillus* and *Mesogloia vermiculata* and are quite different in form from those described by Rosenvinge (1935) on the erect portions of the germlings of S. tortilis which he obtained.

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Text figure 2. a. A group of germlings 4 days old, still showing random orientation. b. A well branched germling 8 days old. In both a. and b. the spore (sp) is still visible but eyespots have disappeared. The line at the top represents a length of 50  $\mu$ .





Text figure 3. a, b. Portions of 10 week old germling with the lateral branches converted into sporangia at z, z, z.

c. Two sporangia to a larger scale. To the right the eyespots (st) in the developing zoids can be seen; to the left the zoids have been shed and the persistent walls of the compartments can be seen. The line at the top indicates the scale of a. and b: that at the bottom the scale of c. In each case the line represents a length of 20  $\mu$ .

The sporangia liberated their swarmers individually leaving empty stretches of filament with the dividing walls still clearly visible (Text figure 3c). The swarmers germinated in a similar fashion to those of the preceding generation, giving rise to a further generation of microscopic plants reproducing by plurilocular sporangia.

Meanwhile the original plurilocular plants continued to increase in size, forming dark brown cushions of irregular shape, about 1 cm. across and producing a succession of plurilocular sporangia. Some of these original plants were kept in culture for 9 months before being lost to a fungal infection, and throughout this period they continued their vegetative growth and production of sporangia.

During this same period, three daughter generations were also produced, but no erect filaments such as obtained by Rosenvinge developed, although in the same period of time on the shore the plants

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had completed their life history to the early stages of sporangium formation.

Exactly comparable behaviour — the formation of a persistent, encrusting cushion producing a succession of sporangia giving further generations behaving in the same fashion — has also been observed by the writer in germlings of *Dictyosiphon foeniculaceus*. I am of the opinion that this behaviour may be the plant's response to adverse conditions, and in nature may be the way in which the plants overwinter. Probably in these experiments inadequate culture conditions — probably too great fluctuations in temperature — have resulted in the prolongation of this microscopic phase and prevented the full expression of the life history.

The germlings obtained by  $R \circ s \in n \vee i n g \in (1935)$  were protonemal in nature and gave rise to erect filaments which remained unseriate but produced hairs and appeared morphologically equivalent, though reduced, to the original macroscopic generation.  $R \circ s \in n \vee i n g \in$  believed that he had obtained the full life history and considered it to be completely asexual without any meiotic divisions. The sporangia produced by this new generation, however, were typical plurilocular sporangia with typical individual release of the swarmers and persistent walls ( $R \circ s \in n \vee i n g e$ , fig. 8D), and thus contrasted strongly with those of the original macroscopic generation which had only evanescent dividing walls and release of the swarmers in the common mucilaginous mass typical of unilocular sporangia.  $R \circ s \in n \vee i n g e$  did not follow the fate of the swarmers of this generation and it seems quite possible that the entire cycle was not obtained.

Kuckuck (1912 p. 166) discussed in deatil interpretation of the sporangia of the macroscopic plant and stated that morphologically they were not clearly either unilocular or plurilocular; but since, in the majority of the plants he handled the swarmers behaved as gametes, he finally concluded that they were plurilocular.

#### CYTOLOGY OF THE MACROSCOPIC GENERATION.

#### I. VEGETATIVE CELL DIVISIONS.

These were seen best in plants grown in vegetative culture. *Stictyo-siphon tortilis* propagates readily by vegetative means, and numerous cultures were established by isolating portions about six cells long from the terminal uniseriate portions of the thallus. These portions grew rapidly in length, becoming multiseriate and producing hairs and lateral

branches which could readily be subcultured in the same way. In this way cultures were kept alive for many months.

The axes of these plants, however, never became very thick, and the surface cells had a pronounced tendency to grow out into long rhizoidallike filaments which ultimately developed an apical cell and continued growth as a normal vegetative axis. By means of these »stolons« a single portion of axis may give rise to a whole tuft of axes and produce the condition described by K j e l l m an (1877 p. 45; 1883 p. 250) as *Stictyosiphon pumila*.

The resting nucleus.

The resting nucleus has a finely granular appearance and a conspicuous nucleolus. It varies somewhat in size with a diameter of 5  $\mu$  in the surface cells, and about 8–10  $\mu$  in the meristematic cells at the bases of the hairs or in the branch initials.



Tetx figure 4.

A series of chromosome counts made on macroscopic plants and germlings of *Stictyosiphon tortilis*. Photomicrographs of these nuclei are shown in Plates II and III: the shaded chromosomes in this figure are those seen in the optical plane illustrated in the corresponding photomicrograph. The number of chromosomes counted is recorded by each nucleus. *A.B.* Two prometaphase nuclei from vegetative cells of the macroscopic plant: c.f. Plate II B & D. *C.D.E.* Mataphase plates at the first division of the sporangial initial: c.f. Plate II G,H,J. F. Metaphase plate at third sporangial divisions: c.f. Plate III B. *G.H.J.* Prometaphase nuclei from vegetative cells of germlings: c.f. Plate III D,E,F. All nuclei to the same scale: the line represents a length of 5  $\mu$ .

#### Nuclear division.

During early prophase the nucleus enlarges and long, slender chromosomes differentiate; these contract first into short rods (Plate II A) and finally to spheres; the nucleolus disappears. After a short prometaphase stage in which the chromosomes are fairly widely separated, a compact and crowded metaphase plate with a conpicuous intranuclear spindle is organised (Plate II C.D). Anaphase separation takes place as two flat plates, and is followed by telophase and constitution of two daughter nuclei.

#### Chromosome counts.

Three nuclei in the prometaphase or metaphase stage were analysed, but in all cases crowding or depth of focus prevented a full count being made. Two of these nuclei are shown in Plate II B and D, and their analysed shown in Text figure 4 A and B. In the three nuclei analysed counts of 44, 40 and 45 respectively were obtained, but in all cases a number of chromosomes remained uncounted.

#### II. THE DEVELOPMENT OF THE SPORANGIA.

A precise account of the nuclear divisions initiating development of the sporangia is essential if an understanding of their nature is to be achieved (see page 9). None of the plants grown in culture produced sporangia, so for this aspect repeated collections of plants from the shore was made. The most numerous early stages in sporangial development were found in plants collected in the second half of May and in early June.

#### The first division of the sporangial initial.

Sporangial initials can readily be distinguished from the vegetative cells. The vegetative cells contain elongated plastids, usually arranged peripherally as seen in surface view, and numerous pyrenoids: the relatively small nucleus occupies a central position. When a cell becomes a sporangial initial the plastids and pyrenoids disappear and the cell contents become homogeneously granular and deeply staining with acetocarmine. This latter property, whilst rendering the initials conspicuous, lessens the contrast in staining between the chromosomes and the cytoplasm. A feature of sporangial development is the tendency for large tracts of surface cells to become converted more or less simultaneously into sporangial initials. The divisions themselves are not completely synchronised and usually a number of stages can be found in any one sorus. The ultimate result is that the sporangia in any one sorus mature within a short time of each other and large numbers of swarmers are shed simultaneously.

During prophase the nucleus increases greatly in volume until its diameter almost equals that of the cell. Chromosomes differentiate as slender threads (Plate II E) and in some there is an appearance of spiral coiling. Early prophase, with conspicuous coiled chromosomes, is prolonged ant often accompanied by polarisation of the chromosomes: the nucleolus persists almost until the end of prophase. The chromosomes contract and shorten, becoming more intensely staining during the process, and sometimes during the later prophase stages and during prometaphase a paired condition of the chromosomes is indicated by clefts in the direction of the longer axis of the chromosomes. This double appearance is quite different from that seen during chromated separation in the vegetative cells when cleavage is *perpendicular* to the longer axis (Plate III H). After a widely spaced prometaphase the chromosomes, fully contracted, become arranged into a very compact metaphase plate with an intranuclear spindle. This plate occupies approximately the same area as that in a vegetative cell, but the components can be seen to be larger (cf. Plate II D & II G). Anaphase separation takes place, as in the vegetative cells, as two flat plates, and is succeeded by telophase and reconstitution of two very lightly staining daughter nuclei.

Six metaphase plates were analysed and gave the following counts: -25, 25, 23, 24, 26, 26. Three of these plates are illustrated in Plate II G, H and J, and their analyses shown in Text figure 4 C, D and E.

Further divisions within the sporangium.

A second division takes place in the sporangium initial before there is any cleavage of the cytoplasm (Plate II A); the daughter nuclei resulting from this division are again very lightly staining.

This division is often followed immediately by a third (Plate III B) and by a fourth (Plate III C), so that en eight-nucleate condition occurs before there is any cleavage of the cytoplasm or septum formation. This feature was figured by Reinke (1889, Taf. 32) and commented on by Kuckuck (1912).

The metaphase plate (1) illustrated in Plate III B was analysed (Text figure 4 F) and gave a count of 26. There is no appreciable diminution in size of the metaphase plate by this four-nucleate stage, but in the later divisions the plates and the chromosomes diminish rapidly in size.

The later stages of division are accompanied by cleavage of the cytoplasm and wall formation: the final divisions take place within the walled compartments. After the final divisions the eyespots developed and the swarmers are organised.

#### CYTOLOGY OF THE GERMLING.

#### The resting nucleus.

The resting nucleus of the germling has a diameter of about 2  $\mu$  and stains intensely with acetocarmine showing a finely granular structure and a conspicuous nucleolus. Before division the nucleolus increases in size.

Vegetative cell division.

During prophase the chromosomes differentiate as long, fine threads which undergo drastic shortening to short rods and ultimately to approximately spherical bodies about 0.5  $\mu$  in diameter. During the prometaphase stage, when the nucleolus and the nuclear membrane have disappeared, the individual chromosomes become fairly widely separated from each other (Plate III D,E,F) and it is sometimes possible to obtain a count at this stage.

A very compact metaphase plate follows (Plate III G), but the chromosomes are too small and too crowded to be counted at this stage. As in Laminaria (N a y l o r, 1956 a) the chromosomes are arranged on the plate with their longer axes parallel to the spindle. An equatorial cleft develops as the chromatids separate, so that the whole has a characteristic dumbell-like shape (Plate III H).

A conspicuous intranuclear spindle is formed and the daughter chromosomes separate as two regular, flat plates (Plate III J). Occasionally one chromosome may lag, but this is not such a regular feature as in Laminaria. Telophase and constitution of two daughter nuclei follow.

Chromosome counts.

Seven prometaphase nuclei were analysed and gave the following counts:— 20, 20, 20, 17, 20, 21, 26. Three of these nuclei are illustrated in Plate III D, E and F, and the analyses are shown in Text figure 4 G, H and T.

Depth of focus may have obscured some of the chromosomes in those nuclei which gave the lower values. The nucleus which gave the count of 26 (Plate III F) was a particularly clear one, so this is probably the value which should be taken.

#### DISCUSSION.

The interpretation of the sporangia of Stictyosiphon tortilis has been the subject of much discussion, and developmental studies alone do not resolve the problem. The usually accepted interpretation is that they are plurilocular.

Plurilocular sporangium development is usually initiated by successive transverse septations to form a row of flat cells — as seen in the germlings obtained in culture — septations keeping pace with the nuclear divisions; unilocular sporangia usually develop by repeated nuclear divisions without any cleavage of the cytoplasm until divisions are completed. In the plurilocular sporangia of Lithoderma (K u c k u c k, 1912, p. 164), however, nuclear divisions are completed, as in unilocular sporangia, before any septation occurs. On the other hand septa are not unkown in unilocular sporangia and are recorded in *Pleurocladia lacustris* (K l e b a h n, 1895).

Thus the sporangia of Stictyosiphon tortilis may be compared in their manner of development either with the plurilocular sporangia of *Lithoderma*, or with the unilocular sporangia of *Pleurocladia lacustris*, and without additional information their nature cannot be determined.

The liberation and fate of the swarmers are also unsatisfactory as criteria. Usually the swarmers of plurilocular sporangia are liberated individually from the compartments, as in *Stictyosiphon soriferus*, or in a steady stream from a single aperture after the dissolution of the internal septa. In *Stictyosiphon tortilis* the thick mucilaginous inner layer to the wall of the sporangium which forms a containing vesicle into which the swarmers are liberated before release into the sea, is much more typical of unilocular than plurilocular sporangia. The germination of the swarmers provides no evidence since they usually germinate asexually.

Probably the only unequivocable piece of evidence which can be used to determine the nature of the sporangium is the type of nuclear division which takes place at its initiation. Detailed cytological information is not available for many species but wherever development of the unilocular sporangium has been investigated in detail, meiosis has been shown to occur at its first division, and, so far, it has not been found at any other stage in the life history except, exceptionally, in the final divisions of the plurilocular sporangia of certain diploid plants of *Pylaiella littoralis* (K n i g h t, 1925).

The initial division of the sporangium of *Stictyosiphon tortilis* shows features which indicate that it is meiotic. These are the enlargement of the nucleus during prophase until it occupies almost the entire cell, the prolonged early prophase stages with long, looped chromosomes often showing polarisation, and, finally, the double appearance sometimes seen at prometaphase.

Chromosome counts of 26 have been obtained at metaphase of the first division within the sporangium and also at the third division. A similar number of chromosomes have been counted in the germlings. The

number of chromosomes in the vegetative cells has not been determined accurately but one count of over 45 has been obtained. During prophase the nuclei of the vegetative cells do not increase in size to the extent seen in the sporangial initials, nor do they show the long, looped chromosomes. It thus seems highly probable that the first division in the sporangia is meiotic and that the sporangia are to be regarded as unilocular.

The only other cytological investigation in the genus Stictyosiphon is that of M at h i as (1935) on S. brachiata (sub Phloeospora brachiata) in which he records meiosis in the unilocular sporangia. The sporangia of S. tortilis resemble the unilocular sporangia of S. brachiata more closely morphologically than they do the undoubted plurilocular sporangia of S. soriferus. M at h i as obtained a count of 10 chromosomes from the later stages of zoid formation in the unilocular sporangia and, in early anaphase of the vegetative cells »twice as many as those in the unilocular sporangia.«

The life history of *Stictyosiphon tortilis* has not yet been sufficiently worked out to show the full cytological cycle.

#### SUMMARY.

- 1. The life history of *Stictyosiphon tortilis* was investigated by means of observations on the shore throughout the year, supplemented by observations on spores grown in culture.
- 2. The germlings obtained in culture lived for several months and reproduced asexually by plurilocular sporangia, but no new macroscopic generations was produced.
- 3. Nuclear divisions were followed in the vegetative cells and developing sporangia of the macroscopic plants and in the vegetative cells of the germlings.
- 4. Chromosome counts of 44<sup>+</sup> were obtained in the vegetative cells of the macroscopic plant, and counts of up 26 in the developing sporangia and the cells of the germlings. These figures, together with the prolonged prophase and appearance of pairing during the first division of the sporangial initial, indicate that this division is meiotic.

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#### NEKI AKSPEKTI RAZVITKA I CITOLOGIJE VRSTE STICTYOSIPHON TORTILIS (RUPR.) REINKE

#### Margaret Naylor

#### Botanički instititut Sveučilišta u Hullu Referirano na sastanku algologa, jula 1957. Institut za oceanografiju i ribarstvo, Split

#### Kratak sadržaj

- 1. Izučavan je razvitak vrste Stictyosiphon tortilis. U tu svrhu vršena su opažanja kroz godine na živim biljkama na obali i ujedno je praćeno klijanje i razvitak spora u umjetnoj kulturi.
- 2. Mlade biljke, dobivene u kulturi, živjele su nekoliko mjeseci i množile su se nespolno pomoću plurilok sporangija.
- 3. Pratili smo diobu jezgre u vegetativnim stanicama i sporangijama makroskopskih biljaka i u vegetativnim stanicama klica.
- 4. U vegetativnim stanicama makroskopskih biljaka nabrojena su 44, a u sporangijama i u stanicama klica do 26 hromozoma. Ovi brojevi i neke druge indikacije upućuju na to, da se tu radi o mejotičkoj diobi.



Plate I.

10 cm



Plate II.



Plate III.

#### EXPLANATION OF PLATES.

Plate I. Photograph of a well grown specimen of *Stictyosiphon tortilis* collected at Filey, May, 1956.

Photograph by W.H. Smithson.

- Plate II. Photomicrographs of nuclear division in the vegetative cells of S. tortilis and in the sporangial initials. A. Late prophase in vegetative cell division showing the chromosomes contracted to short rods. B. Prometaphase in vegetative cell showing the fully contracted chromosomes: an analysis of this nucleus in shown in Text figure 4A. C. Metaphase plate in vegetative cell seen in side view and showing the spindle. D. Polar view of an almost flat metaphase plate in a vegetative cell: an analysis of this plate is shown in Text figure 4B. E. Early prophase in a sporangial initial showing long, looped chromosomes. F. Prometaphase in a sporangial initial showing paired chromosomes. G.H.J. Polar views of metaphase plates at the first division of the sporangial initial: analyses of these plates are shown in Text figure 4 C,D & E. All photomicrographs to the same scale,  $\times$  3,000. The line at the bottom of each photomicrograph represents a length of 10  $\mu$ .
- Plate III. Photomicrographs of later divisions of the sporangial initial and of the vegetative cells of the germling. A. Metaphase at the second division of the sporangial initial showing one plate in side view and one in polar view. B. Metaphase at the third division of the sporangial initial showing two plates in polar view and two in side view: an analysis of plate (1) was made and is shown in Text figure 4F. C. Metaphase at the third division of the sporangial initial showing eight plates (numbered). In neither A,B nor C is there any cleavage of the cytoplasm. D.E.F. Prometaphases in the vegetative cells of the germlings: analyses of these nuclei are shown in Text figure 4G, H & J. G. Metaphase place in vegetative cell of germling in polar view showing the small, crowded chromosomes. H. Metaphase in vegetative cell of the germling seen in side view and showing the dumbelllike appearance of the chromosomes as the chromatids separate by means of an equatorial cleft. J. Early anaphase in vegetative cell of germling showing the separation of the daughter chromosomes as two flat plates. All photomicrographs to the same scale,  $\times 3,000$ . The line at the bottom of each photomicrograph represents a length of 10  $\mu$ .

Plates 1I & III. Prepared by W.H. Smithson from the author's negatives.

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