against the osmotic attraction of the dissolved salts; while the maintenance of equilibrium along the vessels of the balanced osmotic column, with its semi-permeable partitions, demands that an equal amount of water must rise spontaneously to take the place of what is thus removed.

The subject might, perhaps, be further elucidated by observation of the manner in which the flow is first established at the beginning of the season, or possibly by experiments on the rate at which water would be absorbed by a wounded stem high above the ground.

On the Cytology of Apogamy and Apospory.—II. Preliminary Note on Apospory.

By Miss L. Digby.

(Communicated by Professor J. B. Farmer, F.R.S. Received April 15,—Read May 11, 1905.)

Apospory is the direct vegetative process which leads from the sporophyte to the gametophyte without the intervention of spores. This phenomenon has for a long time been known to occur in mosses* and ferns,† and several writers have described its morphological characters, but its cytological history has hitherto remained unrecorded. In a previous note‡ the cellular features of apogamy were briefly described, and it is here proposed to treat the problem of apospory in a similar manner. The following remarks are limited to the study of apospory in *Nephrodium pseudo-mas* Rich. var. *cristata apospora*, Druery,§ but it is of interest to note that within the limits of a (probably) single, but highly variable species, almost all grades of apospory and

* N. Pringsheim, "Vegetative Sprossung der Moosfrüchte," 'Monatsb. Akad. Wiss., Berlin,' July 10, 1876, pp. 425 to 429.

E. Stahl, "Ueber künstlich hervorgerufene Protonema-bildung an dem Sporogonium der Laubmoose," 'Bot. Zeitg.,' vol. 34, 1876, pp. 689 to 695.

N. Pringsheim, "Ueber Sprossung der Moosfrüchte und den Generationwechsel der Thallophyten," 'Jahrb. für wiss. Bot.,' vol. 11, 1878, pp. 1 to 46.

† C. T. Druery, "Observations on a Singular Mode of Development in the Lady Fern (*Athyrium Filix-fœmina*)," 'Jour. Linn. Soc. Bot.,' vol. 21, 1884, pp. 354 to 358 and pp. 358 to 360.

F. O. Bower, "Apospory and Allied Phenomena," 'Trans. Linn. Soc. Bot.,' 2nd series, vol. 2, Part 14, July, 1887, pp. 301 to 326.

‡ J. B. Farmer, J. E. S. Moore, and L. Digby, "Preliminary Note on Apogamy," 'Roy. Soc. Proc.,' vol. 71, 1903, pp. 453 to 457.

§ See "*Lastrea pseudo-mas* var. *cristata apospora*," C. T. Druery, 'Book of British Ferns,' p. 99.

apogamy, with the exception of true parthenogenesis, have been encountered. Our thanks are especially due to Mr. C. T. Druery, who has kindly supplied us with the original fronds, and to the Curator of the Chelsea Physic Garden, who has most carefully cultivated the plants with excellent results.

The aposporal character of *Nephrodium pseudo-mas* var. *cristata apospora* appears to have been first noted by Dr. F. W. Stansfield. It occurred as a sport in a very damp fernery. Our fronds were pegged down in pans of moist earth, and the cultures have been grown in a greenhouse kept at an average temperature of 55° to 60° Fahr. in the winter and of 65° to 70° Fahr. in the summer. It was found that no aposporous growths appear until the fronds have been pegged down, and in each case the fronds were severed from the plant, as this was found to greatly encourage the production of the growths. The aposporous growth is rapid and prolific; fronds treated during the spring and summer showed prothalli, bearing embryos, in three weeks' time. By the autumn these young plants were sufficiently matured to have their leaves layered, and these shortly exhibited the same characteristic feature. It is immaterial as to which surface of the frond is in contact with the soil. So far as has been ascertained this fern remains very constant in character, and continues to breed true. In the plants grown at Chelsea, no trace of a sporangium or sorus has appeared on any of the leaves.

The prothallial growth originates either from the surface, or more frequently from the edge (fig. 1) of the frond. It is at first discernible as a small out-

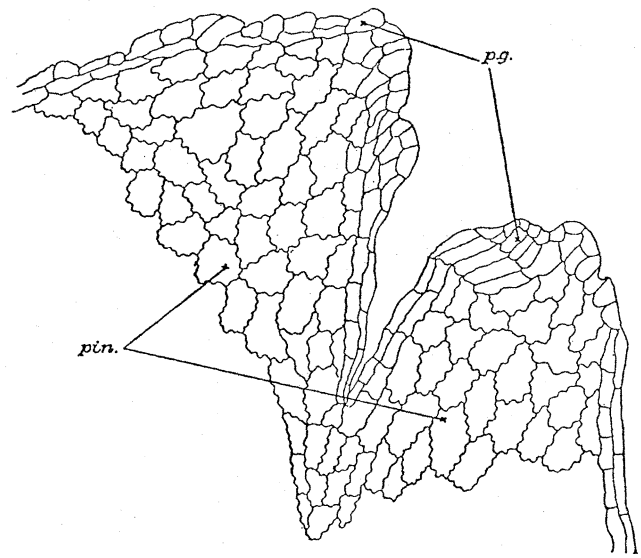

Fig. 1.—Prothallial growth from apices of pinnule. *p.g.*, prothallial growth. *pin.*, pinnule.

growth caused by the division both of the marginal cells of the leaf and of those cells lying immediately within the margin. As the growth proceeds, it is clearly distinguished as a more or less continuous sheet of delicate tissue formed of somewhat rectangular cells. In due course, owing to rapid growth at certain points, the typical prothalloid shape is assumed. The study of many pinnules shows the apex either produced into a single prothallus (fig. 2)

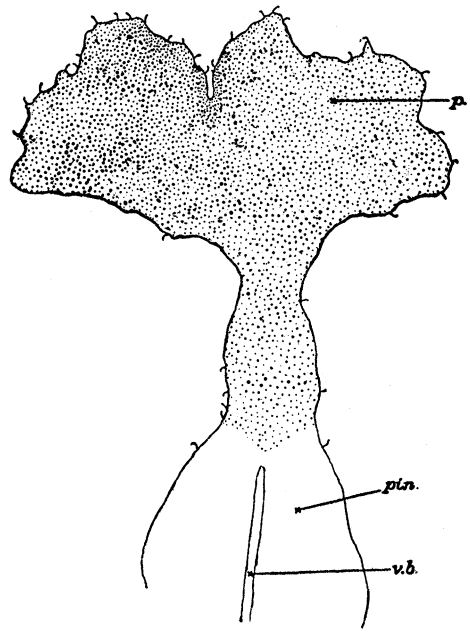

FIG. 2.—Prothallus grown from tip of pinnule. *p.*, prothallus, *pin.*, pinnule, *v.b.*, vascular bundle.

or crowned by a cluster of prothalli, or else the edge is beset with isolated groups. The prothalli on the surface of the leaf may be closely approximated to, or independent of, the vascular tissue. The majority of the prothalli are typically regular in shape, but irregular ones are by no means uncommon. The regular prothalli are normal in appearance, except that they have no well-developed cushion. Antheridia are frequently found, even when the prothalli are comparatively young, but archegonia have never been seen. The prothalli generally show the presence of an embryo in various stages of growth. It is situated in the position normally occupied by the cushion. The irregular prothalli already alluded to vary greatly in shape, and apparently seldom bear antheridia, and never give rise to an embryo.

The principal cytological interest in the prothalli centres in the number of the chromosomes, and in a comparison between the prothallus and the

sporophyte in this respect. The mean of a considerable number of actual countings in the gametophyte is 43 (fig. 3, *a*, *b*, *c*). This calculation is certainly too low owing to the difficulty of realising every individual when dealing with high numbers; 50 is probably nearer the actual figure.

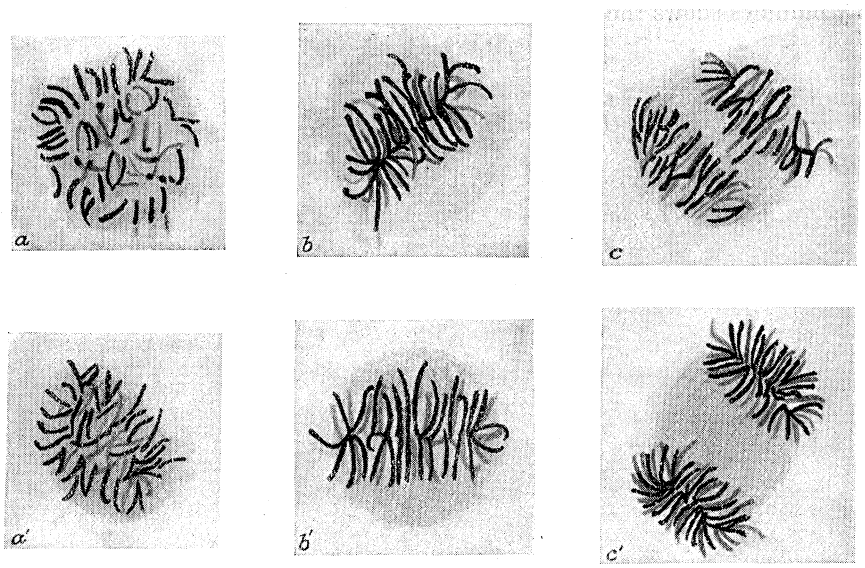

FIG. 3.—Diagrams of nuclear divisions. *a b c* in prothallus. *a' b' c'* in embryo.

The embryo arises as a direct vegetative outgrowth from the prothallus, and, when very young, consists of a rounded mass of cells in which the apical cells of the cotyledon, stem and root, are clearly recognisable. The longitudinal section of an older plant is of a normal type, except for the absence of a foot. The nuclear divisions have been carefully worked out, and, as in the prothallus, the average number of chromosomes present at each mitosis has been taken from several countings. The mean of the numbers obtained is 41, but as in the case of the prothallial nuclei, this is certainly too low (fig. 3, *a'*, *b'*, *c'*). The absolute number is not, however, of great importance, but the close approximation in the results of the chromosome countings of the prothallial and sporophytic nuclear divisions, undoubtedly proves that there is *no reduction* during the transition of the sporophyte to the gametophyte generation. A similar result has been obtained in *Athyrium Filix-fœmina* var. *clarissima* Jones, where the aposporous growth is formed in relation to young but abortive sporangia.* Here, however, the absence of reduction is accompanied by cytological features, indicating a transient

* Bower, *loc. cit.*

condition characteristic of an earlier phase of the heterotypical mitosis, which may throw some light on the anomaly. A discussion of these results will appear in the final memoir. It is interesting to note that Professor Strasburger has placed a similar interpretation on the phenomenon of apogamy in *Eualchemilla*,* which was first described by Murbeck. Here, too, there is no reduction either in the formation of the embryo sac or of the ovum, the latter giving rise, without fertilisation, to the apogamously formed embryo.

The prothalli of the two apogamous varieties, *Nephrodium pseudo-mas* Rich. var. *polydactyla* Wills, and *Nephrodium pseudo-mas* Rich. var. *cristata apospora* Druery, exhibit two striking differences. Whereas in the former nearly all the prothalli, except very young ones, have a strand of vascular tissue extending throughout the greater part of their length, in the latter only two cases of feebly-developed tracheides have been seen. Again, in *Nephrodium pseudo-mas* var. *polydactyla*, migrating nuclei, some of which have been seen to fuse, are a characteristic feature.† Out of a large number of prothalli it was found that about 73 per cent. of the young ones exhibit phases of nuclei passing from one cell to another. As this fern produces fertile spores, it is almost certain (it is hoped shortly to settle this point) that there is a true reduction during the division of the spore mother cells, the doubled number characterising the sporophyte is apparently brought about by the migration and fusion of prothallial nuclei. In *Nephrodium pseudo-mas* var. *cristata apospora*, out of 80 prothalli examined, only two showed possible cases of nuclear migration, and these were open to doubt as regards their interpretation.

The reason for the absence of fusion in other cases is obvious, for the prothalli of *Nephrodium pseudo-mas* var. *cristata apospora*, as we have seen, already possess the full complement of somatic chromosomes. Hence there is no need for the fusion of two nuclei which, by their union, double the number of chromosomes.

I am deeply indebted to Professor J. Bretland Farmer, and to Mr. J. E. S. Moore for their constant help and advice. Professor Farmer has most kindly allowed me to use his material, and has superintended the work throughout.

* E. Strasburger, "Die Apogamie der *Eualchimillen*," 'Jahrb. für wiss. Bot.,' Leipzig, vol. 41, 1904, pp. 88 to 164, Pl. I to IV.

† Farmer, Moore, and Digby, *loc. cit.*

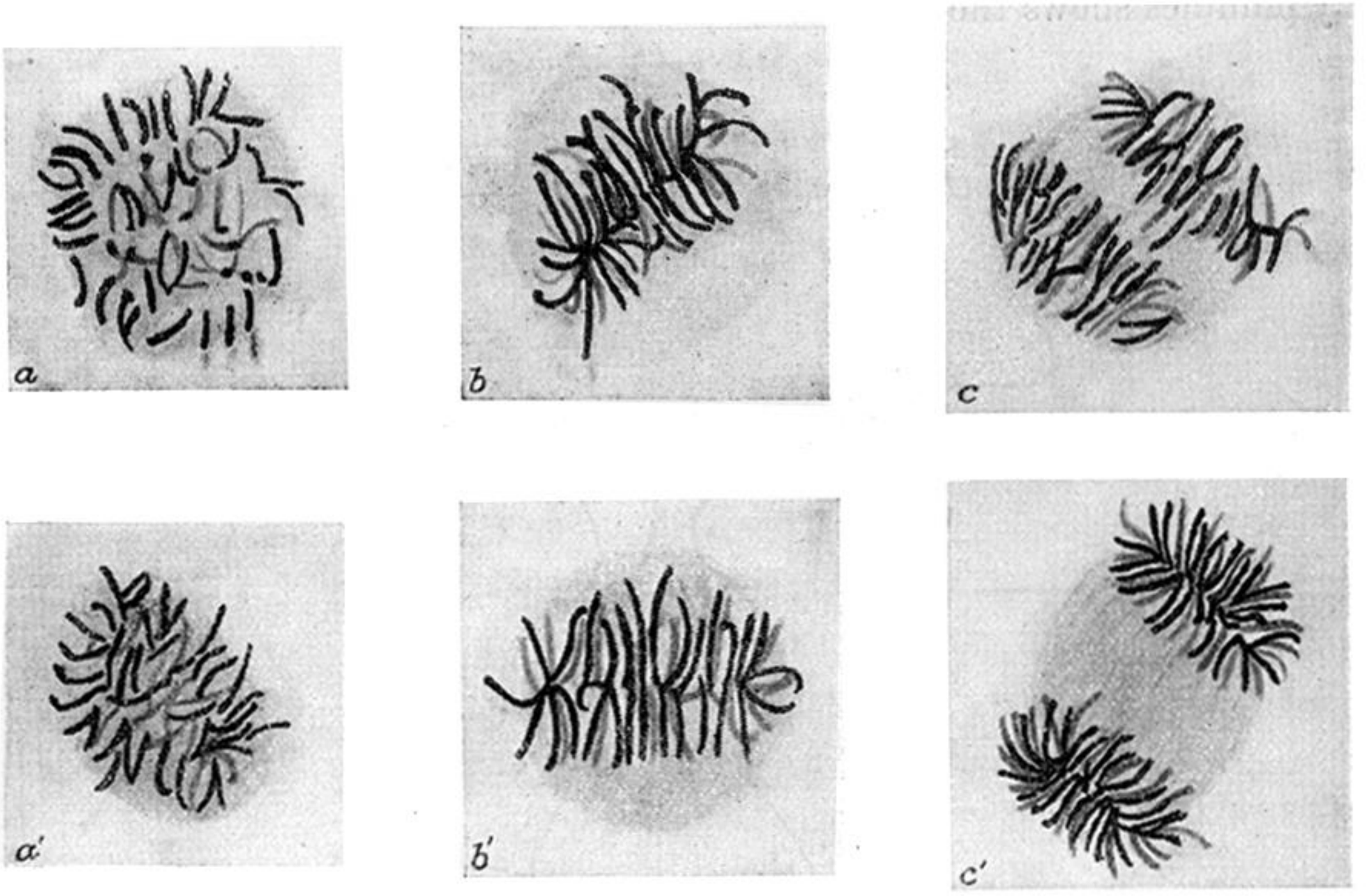

FIG. 3.—Diagrams of nuclear divisions. *a b c* in prothallus. *a′ b′ c′* in embryo.