Note on Vegetative Reproduction in some Indian Selaginellas.

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With Plate XLIX and seven Figures in the Text.

THE two species of *Selaginella* which form the subject of this note were sent as herbarium specimens by Professor Kashyap, of the Lahore Government College, to Professor Seward, who has very kindly handed them to the writer for investigation. Professor Kashyap collected them in the neighbourhood of Rajpur and Mussoorie, India, in August and September, 1913, and they have been identified by Mr. C. H. Wright, of Kew, as *Selaginella chrysocaulos*, Spring, and *S. chrysorrhizos*, Spring.¹

According to Hieronymus,² both species belong to the group of *Selaginella suberosa*,³ a subdivision of the pleiomacrosporangiate and monostelic Heterophylleae. In his diagnosis of the group, Hieronymus notes that apparently vegetative reproduction is not normally present, and the representative species reproduce themselves only by spores; Spring does not especially mention any methods of vegetative reproduction, though the presence of stolons at the base of the vegetative stems seems to be a characteristic of *S. chrysocaulos*.⁴

The chief interest of the two specimens under consideration lies in the fact that they show vegetative reproduction, this being normally unrepresented in the group to which they belong, although similar types of reproduction regularly occur in other forms.

The specimens of *S. chrysocaulos* are characterized by the possession of bud-like structures at the tips of some of the vegetative branches (Pl. XLIX, Fig. 1, and Text-fig. 1). Professor Kashyap refers to them as 'surface tubers', their function being propagative. Hieronymus⁵ notes that in *Selaginella Lyallii*, *S. Vogelii*, and related species, a transformation of

¹ For the localities of these two species see Spring's Monographie de la famille des Lycopodiacees, Pt. II. Mém. de l'Acad. Roy. de Belgique, t. xxiv, 1850, pp. 250, 251.

² Hieronymus, G. Selaginellaceae (in Engler and Prantl's Pflanzenfamilien, I, 4, ii, p. 621, 1900), p. 626.

³ Spring considers the two species as closely related to one another and to *S. suberosa*.

⁴ Spring, l. c., p. 250.

⁵ Hieronymus, l. c., p. 666.

the apex of a vegetative shoot may take place. The observations of Bruchmann¹ show that in *S. Lyallii* the branches of the older shoot-systems close to the ground, or branches of the ordinarily erect system

TEXT-FIG. 1. *Selaginella chrysocaulos*. A 'surface tuber', showing the dichopodial branching, the occurrence of the ventral rhizophores, and the arrangement and form of the leaves. The enlargement of the end of a rhizophore before branching, with a considerable development of root-hairs, is indicated at A. $\times 3$.

accidentally in contact with the ground, may become enlarged at the apex and form leaves which differ considerably from the leaves of the ordinary branches, resembling the scales on the rhizome and on the lower unbranched parts of the erect system.²

In *S. chrysocaulos* the stem-apices forming the 'buds' or 'tubers' show close and repeated dichotomous ('dichopodial'³) branching; a rhizophore often occurs in the fork between two branches, arising in the axil of a leaf (Pl. XLIX, Fig. 1, and Text-figs. 1 and 2).⁴ The rhizophores are themselves frequently dichotomously branched (Text-fig. 1), and serve to attach the 'tubers' firmly to the substratum. In several cases the commencement of branching is indicated by the enlargement of the end of the rhizophore⁵ (Text-fig. 1, at A). Particularly at such

enlargements, the tips of the rhizophores develop very numerous root-hairs, the epidermal cells growing out to some length. This also is indicated at A in Text-fig. 1.

The leaves of the tubers are very closely packed and uniform in size; they are relatively broader and shorter than the leaves of the erect system, and possess a very distinct awn, about one-quarter to one-third of the

¹ Bruchmann, H.: Die vegetativen Verhältnisse der Selaginellen (Giebel's Zeitschr. f. d. gesamt. Naturwissensch., 1877, i, pp. 524-6), p. 526.

² Bruchmann also showed that cones may proliferate in the same way; and Behrens (Über die Regeneration bei den Selaginellen, Flora, lxxxiv, 1897, p. 159) produced proliferated apices artificially in various species, obtaining new plants from them.

³ Cf. Velenovský, J.: Vergleichende Morphologie der Pflanzen, 1905-13, p. 246 and p. 259, Fig. 177.

⁴ Hofmeister, W.: On the Higher Cryptogamia (trans. by F. Currey; Ray. Soc., 1862), p. 383.

⁵ Ibid., p. 384.

length of the leaf, this being absent in the ordinary lateral or ventral leaves, though present in the dorsal leaves. The margins of the tuber leaves are

TEXT-FIG. 2. *S. chrysocaulos*. A, B, and C show diagrammatically a series or stages in the branching of a 'surface tuber', with the separation of the ventral rhizophore (v.), subtended by its axillary leaf (a.l.). br.v.s., vascular supply of the vegetative branches; v.v.s., vascular supply of the ventral rhizophore. $\times 30$.

also very minutely ciliate,¹ ciliation being present elsewhere only on the upper basal margin of the ventral leaves.

The dried material was prepared for sectioning by treatment with lactic acid. Microtome sections (10μ thick) were cut in the case of four tubers,

¹ This is not shown in the figure.

but the anatomy was not found to be in any way unusual, the distribution of the vascular system being the same as in ordinary branching of the stem in monostelic forms.¹

Text-fig. 2, A, B, and C, from a series of transverse sections through a tuber, shows the forking of the axis and the formation of the ventral rhizophore with its subtending 'axillary' leaf. The rhizophore is well developed and separates immediately after the branching of the axis (Text-fig. 2, B).

Text-fig. 3 shows one of a series of sections in which a small dorsal protuberance appears just before the dichotomy of the axis; this is the

TEXT-FIG. 3. *S. chrysocaulos*: Diagrammatic transverse section of a 'surface tuber', just below the separation of a branch. *d.*, the dorsal rhizophore; *d.v.s.*, the vascular supply to the dorsal rhizophore; *br.v.s.*, the vascular supply to the branch. $\times 30$.

undeveloped rudiment of the dorsal rhizophore.² A slender vascular trace is given off towards it immediately before the bifurcation of the stele (Text-fig. 3). Thus the order of appearance of the vascular supplies at the bifurcation of the stem is as follows: dorsal rhizophore, branch, ventral rhizophore.³

The specimens of *Selaginella chrysorrhizos* exhibit a type of vegetative reproduction which is apparently typical for *S. bulbilifera*. Hieronymus⁴ re-

marks that bulbil structures have only been observed as a regular phenomenon in *S. bulbilifera*, and are found both at the apices of cones and of vegetative branches, the latter sometimes becoming elongated and filamentous. They are small bulb-like organs of propagation which consist of a so-called 'leucus' or corm—a swelling of the apex of the shoot caused by hypertrophy of the cortical parenchyma. This tissue is filled with reserve materials, and the whole structure is closely surrounded by numerous crowded leaves, spirally developed and somewhat swollen at the base, but otherwise very similar to the early leaves of many species. The vegetative apex of the bulbils divides once or twice while these are still on the plant, in the same direction as dichotomies take place in the rest of the plant.

¹ Cf. Harvey Gibson, R. J.: Contributions towards a Knowledge of the Anatomy of the Genus *Selaginella*, Pt. I, The Stem. Ann. of Bot., vol. viii, 1894, p. 133.

² Treub, M.: Recherches sur les organes de la végétation du *Selaginella Martensii*, Spring, 1877, p. 12.

³ Harvey Gibson, l. c., Fig. 53. This figure of *Selaginella inaequalifolia* shows the axillary leaf subtending the ventral rhizophore. It also shows that the dorsal rhizophore arises slightly before the ventral rhizophore.

⁴ Hieronymus, l. c., p. 666.

Vegetative branches of *S. chrysorrhizos* show this type of bulbil formation. Some of the lower branch-systems of the plants become elongated and filamentous, their leaves being much reduced, scale-like, and scattered (Plate XLIX, Fig. 2, and Text-fig. 4). In some cases the ends of these branches penetrate underground and become enlarged, developing numerous closely crowded, colourless scale leaves (Pl. XLIX, Fig. 2, and Text-fig. 4; also Text-fig. 6). Professor Kashyap refers to the structures so formed as 'underground tubers', in contradistinction to the 'surface tubers' of *S. chrysocaulos*.

Sections (10μ thick) were cut of tubers prepared with lactic acid, as in the case of *S. chrysocaulos*. These showed a large increase in the parenchymatous tissue at the ends of the branches, the cells usually being densely

TEXT-FIG. 4. *Selaginella chrysorrhizos*. An 'underground tuber' showing the crowded scale leaves. Branches are indicated at B, and root-hairs developed from rudimentary rhizophores at A. The position of the tuber with regard to the elongated, filamentous vegetative branches springing from the base of the plant is also shown. $\times 4$.

filled with reserve food materials. The vascular tissue is comparatively small in amount, and in many cases lignification is not very strong, the two lateral protoxylems only being well differentiated. Text-figs. 5 and 6 indicate the relatively small amount of vascular tissue present. The characteristic trabecular endodermis of the stem-stele may be recognized in the tubers (Text-figs. 5 and 6), as well as in the filamentous vegetative branches. The scale leaves of the stem-apex overlap closely (Text-figs. 4 and 6), their bases often being rather enlarged and containing reserve materials.

The tubers are dorsiventral in organization, and branching takes place repeatedly as in the surface tubers. A dichopodium is formed, the branches on alternate sides being more strongly developed; ¹ the 'lateral branches' thus formed are very short (Text-fig. 5, A and B, from a series of transverse sections of the same tuber; also Text-fig. 6, A and B, from another tuber).

¹ Cf. Hofmeister, l. c., p. 382.

At each dichotomy of the tuber axis, and in the plane at right angles to it,¹ arise two very short branches, which are really exogenous in origin but present a semi-endogenous appearance due to the general enlargement and hypertrophy of the tissues of the tuber (Text-figs. 5 and 6).

The vascular supply to the dorsal branch separates from the stele of the tuber immediately before its bifurcation to supply the two vegetative branches. The ventral branch is subtended by a leaf, and its vascular

TEXT-FIG. 5. *S. chrysorrhizos*. A and B show diagrammatically two transverse sections of an 'underground tuber', A near the base, and B near the apex. br., branch; d., dorsal rhizophore; v., ventral rhizophore; st., stele of axis; br.v.s., vascular supply to branch; v.v.s., vascular supply to ventral rhizophore; r., root-hairs; e., trabecular endodermis. In B the dorsal rhizophores accompanying both branches do not appear at this level. $\times 32$.

supply arises from one branch of the stele immediately after bifurcation has taken place. These short branches are undoubtedly the rudimentary dorsal and ventral rhizophores, which remain short and undeveloped since the tubers are already embedded in the ground. The vascular supply, in its passage to the rhizophores, has the characteristic endodermis of the stem-stele.

The rhizophores have somewhat enlarged rounded ends; a similar enlargement in ordinary rhizophores is, according to Hofmeister,² due to

¹ Cf. Velenovský's description of 'tetrachotomy', l. c., p. 260.

² Hofmeister, l. c., p. 384.

the commencement of furcation and was noted in *S. chrysocaulos*. Text-fig. 5, A, shows a distinct appearance of dichotomy of the rhizophore heads. The epidermal cells of the ends of the rhizophores grow out into long root-hairs (Text-figs. 5, 6, and 7), which are often so much developed as to appear to the naked eye as masses of hyphae (Text-fig. 4, at A; cf. the development of root-hairs at the ends of rhizophores in *S. chrysocaulos*, Text-fig. 1).

TEXT-FIG. 6. *S. chrysorrhizos*. A and B show diagrammatically two transverse sections of an 'underground tuber'. The lettering is the same as in Text-fig. 5. This tuber shows very clearly the closely-overlapping scale leaves (l.). In A continued growth of the dorsal rhizophore is indicated. $\times 32$.

TEXT-FIG. 7. *S. chrysorrhizos*. Longitudinal section of the end of a rhizophore, showing the development of the epidermal cells forming root-hairs. The central area, in which the root-hairs are not developed, is clearly indicated. $\times 275$.

A similar formation of root-hairs was noted by Sarauw,¹ who grew species of *Selaginella* over distilled water. The swollen ends of the rhizophores produced root-hairs about 3 mm. long, forming at first a little disc and later appearing as a short brush, the hairs of which were arranged

¹ Sarauw, G. F. L.: Versuche über die Verzweigungs-Bedingungen der Stützwurzeln von *Selaginella*. Ber. der deutsch. bot. Ges., Bd. ix, 1891, p. 63.

something like the sterigmata of an *Aspergillus* conidiophore head. Sarauw mentions that there was possibly a small area in the centre of the enlarged rhizophore heads without root-hairs; Text-fig. 7 shows this in one of the tubers of *S. chrysorrhizos*. In one case the rhizophore seems to have continued its growth for a short distance from this area, leaving the root-hairs as a lateral flange or collar near its base (Text-fig. 6, A).

CONCLUSION.

The reproductive 'tubers' in these two species of *Selaginella* are fundamentally similar, the differences between them being dependent upon physiological causes, arising from the position of the tubers on the plant.

In *S. chrysocaulos* the tubers are at the ends of ordinary vegetative branches and remain at the surface of the ground, the development of ventral rhizophores being necessary for their attachment to the substratum. The leaves of these tubers, though differing in form and size from those of the ordinary branches, contain abundant chlorophyll. In the case of *S. chrysorrhizos*, on the other hand, the tubers are developed underground at the ends of filamentous, modified vegetative branches. The leaves are scale-like and without chlorophyll, their bases and the tissues of the tuber containing reserve materials, the storage of which is unnecessary in the chlorophyll-containing surface tubers.

Further, in the case of *S. chrysorrhizos*, both dorsal and ventral rhizophores are developed, but they remain very short, since the tubers are already embedded in the ground and elongation of rhizophores is not needed for purposes of attachment. They are fairly equally developed, being subjected to the same developmental conditions, and both are apparently functional in obtaining nutritive elements from the soil by means of the root-hairs developed from their enlarged ends, probably as a response to nutritive stimuli.¹

The dorsal and ventral rhizophores of *S. chrysocaulos*, on the other hand, encounter different conditions from the commencement of their development; for instance, the ventral rhizophores are subjected to less light intensity and greater humidity than the dorsal rhizophores, owing to the position of the tubers on the surface of the ground. The ventral rhizophores alone are functional in attaching the tubers and for nutritive purposes; they attain a considerable development, while the functionless dorsal rhizophores are very much reduced, more so even than in *S. chrysorrhizos*.

The writer desires to express gratitude to Professor Seward for per-

¹ Sarauw, l. c., p. 65; the branching of the rhizophores is said to be due to the dampness of the ground, while the nutritive content of the medium is responsible for their further development.

mission to carry out this investigation at the Botany School ; to Mr. Tansley for helpful advice ; and to Mr. C. H. Wright for the identification of the material described above.

BOTANY SCHOOL, CAMBRIDGE,
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EXPLANATION OF PLATE XLIX.

Illustrating Miss Bancroft's paper on Vegetative Reproduction in some Indian Selaginellas.

- Fig. 1. *Selaginella chrysocaulos*. Habit photograph.
Fig. 2. *Selaginella chrysorrhizos*. Habit photograph.
Both slightly reduced.

2.

1.

Bancroft, Nellie. 1914. "Note on vegetative reproduction in some Indian Selaginellas." *Annals of botany* 28, 685–693.

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