THE SPORELING OF *CERATOPTERIS*[*]

by

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ABSTRACT

CHIANG, Y. L. and SU-HWA CHIANG. (National Taiwan University, Taipei) The sporeling of *Ceratopteris*. Taiwania 8: 35-50. 1962.

The organography and anatomy of the sporeling of *Ceratopteris* (*C. thalictroides* and *C. pteridoides*) are described. Unlike the adult sporophyte which has a greatly reduced stem known as the leafy stem, the sporeling of this fern has an elongated, more or less erect stem with nodes and internodes. It is snggested that light is an important factor affecting the internode elongation. The major parts of the plant body in the sporeling are: primary root, adventitious root, node, internode, hypocotyl, epicotyl, cotyledon, leaf, and terminal bud. The vascular system is extremely simple; only a single strand of vascular tissnes runs through the whole plant body except in the laminum where the bundle forms a network. The stele is a protostele. Evidence is presented showing that the plant body of the sporeling is an aggregation of phytons. The adult phytons, each of which has a complete set of the three fundamental parts (*i.e.*, leaf, stem, and root), are joined one after another with the short interconnecting strand of vascular tissues. The nature and origin of the interconnecting vascular strand are described. The stem of the phyton, which is morphologically the basal part of the leaf, contributes as an internode to constitute the whole plant body. The sporophyte of this fern is thus considered to be a complex organism. The new phytons are derived from the apical phyton initial, or the apical cell of the shoot which is located at the extreme tip of the shoot apex. It is suggested that the apical phyton initial is closely homologous to the zygote, and the apical meristem of the shoot to the young embryo. From this it is further suggested that the embryo at the quadrant stage consists of the apical phyton initial, the two-celled cotyledonary phyton (one cell gives rise to the cotyledon and primary root, and one cell to foot), and the one-celled first phyton. The newly formed juvenile phytons as well as the apical phyton initial are nutritionally and probably hormonally dependent on the prothallus and adult phytons.

AN AQUATIC fern, *Ceratopteris* is a monotypic genus in the family *Parkeriaceae*. An adult sporophyte consists of leaves, roots and a greatly reduced stem known as the leafy stem. In the sporeling, however, the stem is more or less erect, and has nodes and internodes. The internodes are more elongated especially in the plant grown under certain conditions of the environment. Owing to the extreme simplicity in its organography and anatomy, and to the visibly discrete phyton units, the sporeling of this fern provides excellent material for studying the nature of the plant body and its basic structures which has long been a fundmental problem in plant morphology. In the present paper, the organography and anatomy of the sporeling of *Ceratopteris* are described, since they have been previously only briefly studied (Kny, 1875; Ford, 1902; Yabe and Yasui, 1913; and Javalgekar, 1960). Secondly, some evidence is set forth and discussed to prove the phytonic constitution of the plant body of this fern.

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MATERIALS AND METHODS.—The sporelings of *Ceratopteris thalictroides* (L.) Brongn. and *Ceratopteris pteridoides* (Hook.) Hieron. used for the present investigation were obtained from the aquaria in an uncontrolled greenhouse of the Botany Department of National Taiwan University and from cultures in Petri-dishes. The cultures were grown from spores on pieces of unglazed porous plates immersed in water in Petri-dishes under continuous white fluorescent light (far-red weak) in a controlled culture room (20°C±0.5°C). After germination (*i. e.*, few days after sporing) the dishes were removed to a laboratory room and placed by the window. Hoagland's inorganic nutrient solution was occasionally added. The original materials of *C. thalictroides* and *C. pteridoides* were collected by Dr. Charles E. DeVol a few years ago from Chiai, Taiwan (Formosa) and from the Taipei Zoo respectively. The latter species is a newly found species in Taiwan and we are still uncertain whether it is a native species in Taiwan or not. For anatomical study, materials were fixed in Nawaschin fluid. After imbedding in paraffin, sections were cut at 8 or 12 μ and stained with Delafield's haematoxylin.

RESULTS AND DISCUSSION.—*General organography.* The stems of the adult sporophyte of the leptosporangiate ferns belong to either one of the following two types: one is a horizontal rhizome; and the other is a short, erect, aerial stem which appears to be a collection of leaves, or leafy stem. The stem of the adult sporophyte of *Ceratopteris* belongs to the latter type. Unlike the adult plant, the sporeling has an erect, aerial stem with nodes and elongated internodes, and looks very like a

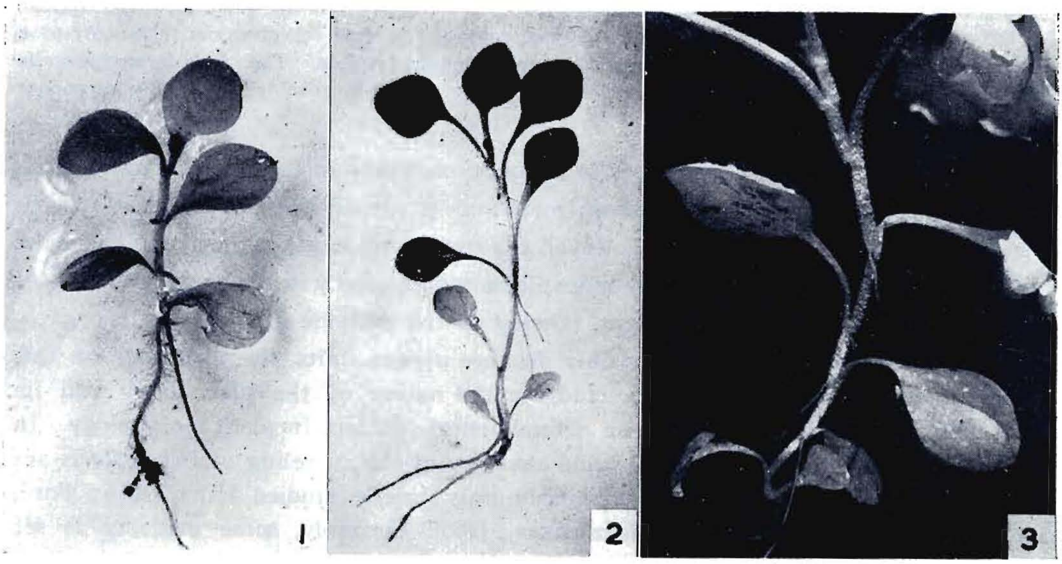
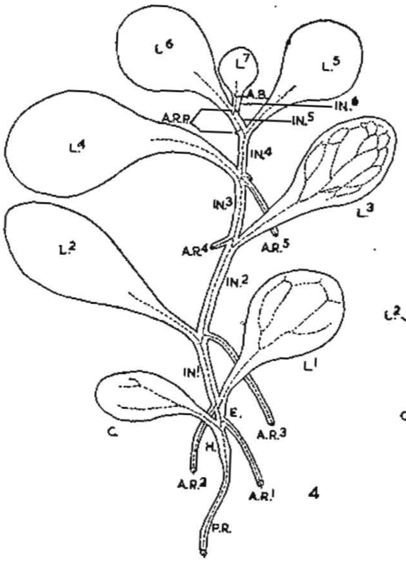


Fig. 1-3. Sporelings of *Ceratopteris*, showing general organography. Note elongated internodes. —Fig. 1. *C. pteridoides* from an aquarium in a greenhouse. The plant was rooting in mud, growing under the shade. ×2.5.—Fig. 2. *C. pteridoides* from a Petri-dish culture. ×2.—Fig. 3. *C. thalictroides* from a Petri-dish culture. ×4.

common young plant of the angiosperms at first glance (Fig. 1, 2, 3). It is this uncommon extermal feature that has greatly aroused our interest. The general organography of the sporeling is shown in various figures in the text (Fig. 4, 7, 14–21). The following structures are recognized in a sporeling: a primary root, adventitious roots, nodes, internodes, a hypocotyl, an epicotyl, a cotyledon, leaves, and a terminal bud. As will be discussed later in detail, the phyton is recognized in the sporeling as the basic unit of the plant body (Fig. 6, 9, 11). Each fully developed phyton consists of three fundamental parts: leaf, stem and root (Fig. 11).

Leaves. The leaf is the principal part of the phyton (Fig. 6, 9). It is sessile, although some degree of differentiation of a petiole can be recognized especially in *C. thalictroides*, at the point or node where the younger, or next phyton is joined (Fig. 4, 7). The leaf arrangement is alternate. Axillary buds and stipules are absent. The scale-like, delicate one-cell thick ramenta are present instead of stipules (Fig. 37). These ramenta are the protective structures of the young developing phytons, and originate in the growing point of the shoot (Fig. 43, 45). All leaves are simple. The successive change in leaf-shape from spatulate to rhomboic and then to lobed accompanied by the growth of the sporeling was observed in *C. thalictroides*, but not in *C. pteridoides*. The younger the sporelings are, the more difficult it is to distinguish among these two species (Fig. 14–21), indicating the close phylogenetic relationship between these two species. The leaves are netted veined except the cotyledon, the first leaf and the second leaf (Fig. 4, 7, 14–21). They are succulent and green with a smooth surface. All leaves found in the sporeling are sterile, whereas in the adult plant they are dimorphic. No vegetative, or adventitious buds occur on the leaves of the sporeling, while they are abundantly formed on the adult sporophyte. The leaves of the sporeling of *C. thalictroides* have been shown by Kny (1875), Yabe and Yasui (1913) and Javalgekar (1960). No significant difference can be noted between their plants and our's, although the adult plant of our local species differs from the species which was described by Kny (1875) on the stipe base characteristic (*i. e.*, the Taiwan species is erect, while Kny's species is horizontal).

The internal structure of the young leaves is shown in Fig. 53–56. The bundle number in the petiole is variable with the age of leaves. The leaves formed earlier have a single bundle in the petiole, while the later leaves (*i.e.*, from about the 6th leaf) have two. The transection of the young petiole is triangular in shape (Fig. 53), but gradually becomes flatter toward the blade. The leaves are composed mainly of spongy tissue with many large air spaces. The epidermal cells, as well as the cells of the inner spongy tissue, contain abundant chloroplasts. This is also true in many polypodiaceous ferns and in a number of higher plants grown in shady or aquatic habitats. Stomata are present on both sides of the blades and petioles. There are about 12 per 1 mm^2 on the adaxial surface of the blades. Only a few stomata are found on the abaxial surface of the blades and on the petioles.



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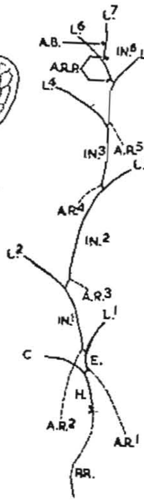

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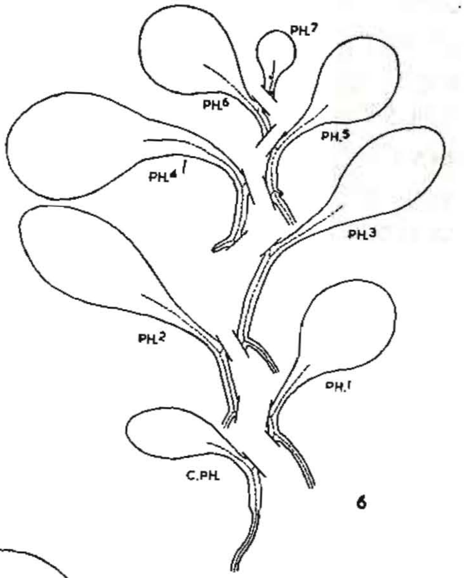

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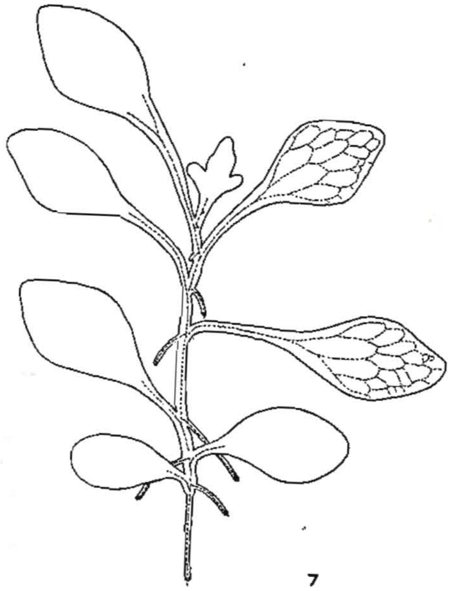

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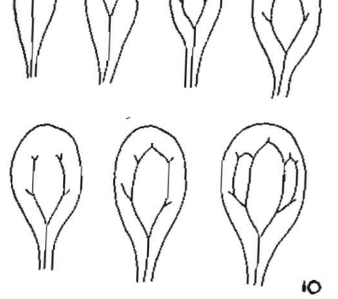

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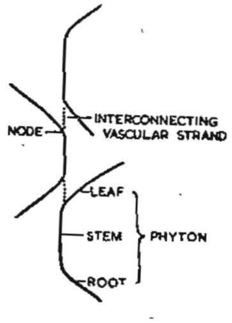

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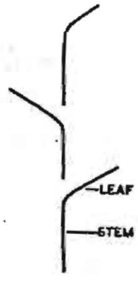

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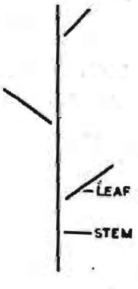

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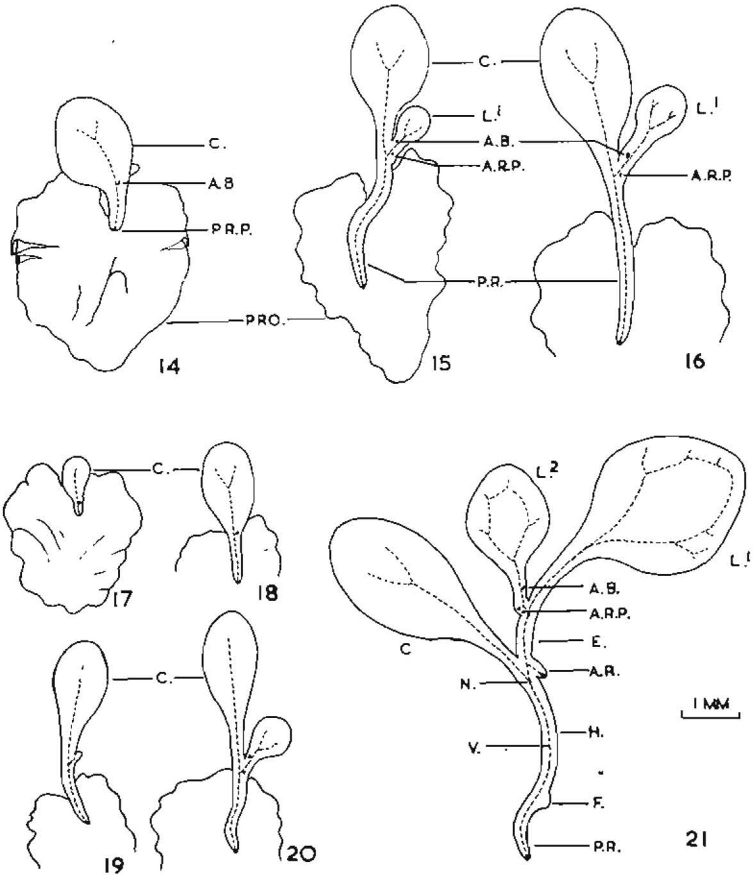

Fig. 14-21. Semi-diagrammatic illustration of organography and vascular system in sporelings of *C. thalictroides* and *C. pteridoides*. All ×10. A. B., apical bud or terminal bud; A. R., adventitious root; A. R. P., adventitious root primordium; C., cotyledon; E., epicotyl; F., foot; H., hypocotyl; L., leaf; N., node; P. R., primary root; PRO., prothallus; V., vascular bundle.—Fig. 14-16. *C. pteridoides*.—Fig. 17-21. *C. thalictroides*.

Stem. The main parts of the stem are nodes, internodes, a hypocotyl, an epicotyl and an apical bud. A node is commonly defined as that point of a stem from which a leaf arises. This definition is obviously based on the enation theory which claims

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Fig. 4-13.—Fig. 4-9. Semi-diagrammatic illustrations showing organography, vascular system and phytonic constitution of the plant body in *Ceratopteris* sporelings. All ×4.—Fig. 4-6. *C. pteridoides*. A. B., apical bud or terminal bud; A. R., adventitious root or adventitious root trace; A. R. P., adventitious root primordium; C., cotyledon; E., epicotyl; H., hypocotyl; IN., internode; L., leaf or leaf trace; PH., phyton; P. R., primary root; x, place where prothallus attached, or foot.—Fig. 4. Organography and vascular system. Dotted line illustrates the vascular strand.—Fig. 5. The vascular system of the sporeling which is depicted in Fig. 4. Dotted line indicates root trace.—Fig. 6. Separation of the sporeling which is depicted in Fig. 4 into phytons.—Fig. 7-9. *C. thalictroides*.—Fig. 10. Venation, showing successive stages of network formation. ×4.—Fig. 11-13. Diagrammatic illustrations showing different views of the constitution of the plant body.—Fig. 11. Phytonic constitution of the plant body in *Ceratopteris* sporeling.—Fig. 12. Goethe's explanation.—Fig. 13. Wolff's explanation.

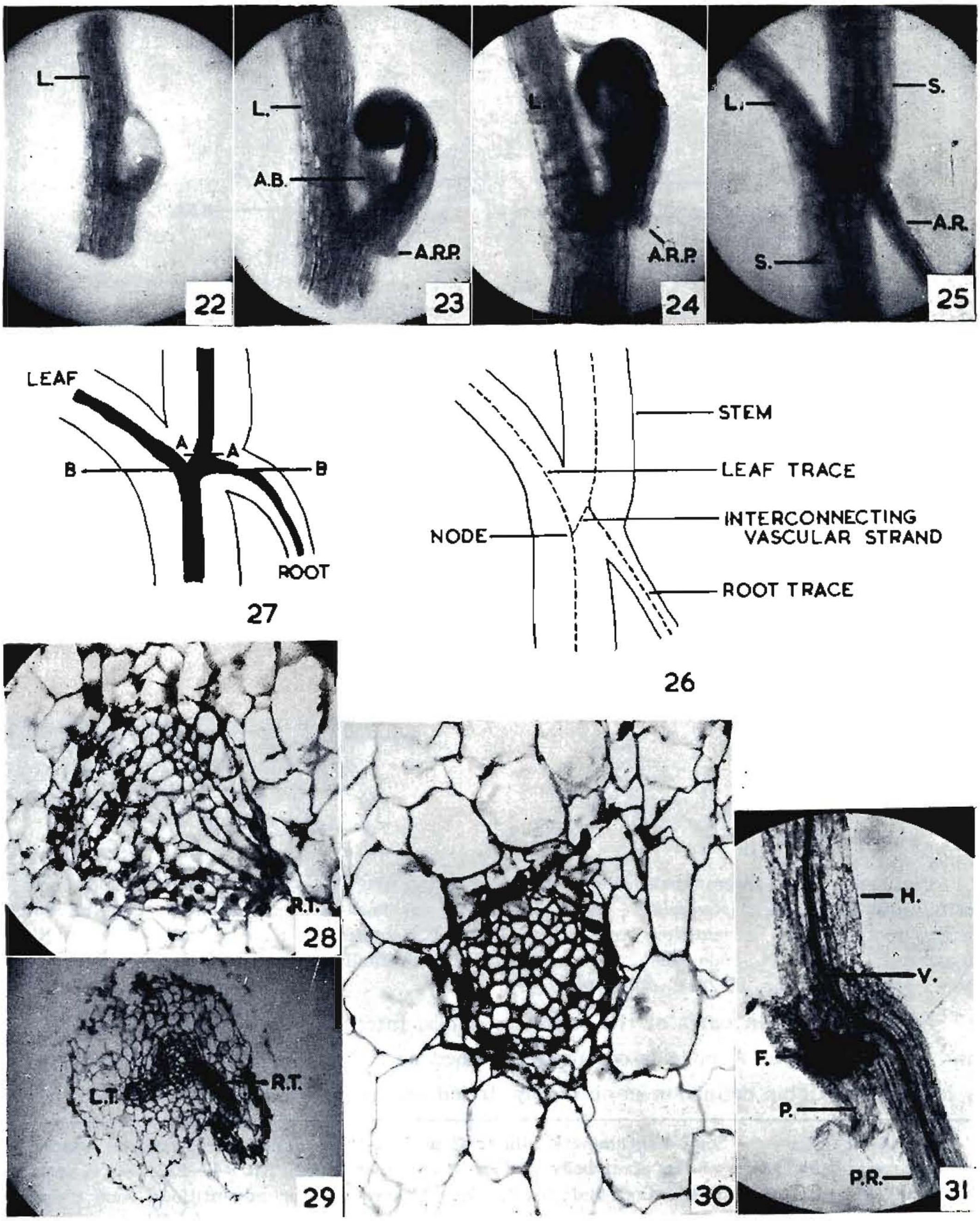


Fig. 22-31.—Fig. 22-24. External structures of terminal buds in *C. thalictroides*, showing successive stages of growth of a newly formed phyton. A. B., apical bud; A. R. P., adventitious root primordium; L., leaf. ×10.—Fig. 25-26. Nodal morphology of *C. thalictroides*. ×10.—Fig. 25. External view of a nodal region. A. R., adventitious root; L., leaf; S., stem—Fig. 26. Diagrammatic illustration of internal structures of the nodal region shown in Fig. 25.—Fig. 27-29. Nodal anatomy of *C. pteridoides*.—Fig. 27. Diagrammatic illustration showing leaving of root trace and leaf trace in longitudinal section. ×10.—Fig. 28. Transection at the level AA in Fig. 27. R. T., root trace. ×195.—Fig. 29. Transection at the level BB in Fig. 27. R. T., root trace, L. T., leaf trace. ×93.—Fig. 30. Transection of stele in *C. pteridoides*. ×210.—Fig. 31. Longitudinal transparent view through the transition region of primary root and shoot in *C. pteridoides*. F., foot; H., hypocotyl; P., prothallus; P. R., primary root; V., vascular bundle. ×12.

that the leaves are the production or appendages of the stem. As shown and discussed in more detail later each internode of the sporeling of *Ceratopteris* is a secondary structure transformed from the leaf base of each phyton (Fig. 6, 9, 11). The node is therefore a point where two adjacent phytons are joined together (Fig. 26). The external morphology of a nodal region is shown in Fig. 22–25, where the boundary between two adjacent phytons are very clearly recognized. The internode is fleshy, green and cylindrical, about 0.5 to 1 millimeter in diameter. The hypocotyl is the stem of the cotyledonary phyton, while the epicotyl is that of the first phyton. A terminal bud is located at the tip of the stem. No lateral buds or branches are found on the stem. As the plant grows larger it may become somewhat decumbent as it has an insufficinet stele or strengthening tissue to support it. However the tip of the stem is always upright. The stem is thus negatively geotropic just the same as in heigher plants. It is also positively phototropic.

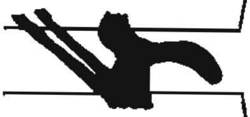
Roots. A primary root and adventitious roots occur in a sporeling (Fig. 4, 7). The primary root, which belongs to the cotyledonary phyton, develops from the hypocotyl. The adventitious roots always arise from the point on the stem slightly above the node (Fig. 26). One root is typically formed at the base of each internode, or morprologically correctly, at the base of each leaf. Thus, the number of roots on a sporeling corresponds very closely to that of the leaves. This has been interpreted by Vladesco (1935) as giving strong support to the phyllorhize theory of Chauveaud (1921) (cited in Wardlaw, 1955). The leaf and root of the same phyllorhize or phyton are always found oriented on the same side, demonstrating the positional relationship between these two organs. A root arises from a single root apical cell which is a large conspicuous cell with the form of a three-sided pyramid (Figs. 39, 51). The root has a profusion of root hairs after it grows to a certain length (Fig. 1). No visible lateral root or secondary root arises from the primary root and the adventitious root, although secondary root primordia can be observed near the tips but this only under the microscope. Mahabalé (1948) reported the secondary root initial in the young embryo of *C. thalictroides*. The present authors consider that the initial he observed is probably that of the first adventitious root. The structure of the transition region between the hypocotyl and the primary root is extremely simple. No difference between them can be noted except that the diameter of the root is about half that of the stem (Fig. 31). There is no morphological difference between the primary and adventitious roots.

Stelar anatomy. The stem of the sporeling (less than one inch in height) of *Ceratopteris* has a protostele. Ford (1902) studied the stem of the young plant of *C. thatictroides* (2 to 4 inches in height), and reported that it is polystelic (2 to 5 strands). We also observed the polystelic sporophytes which were always larger than one inch. Obviously the number of the strands is quite variable with the age of the plants. A transection of the stele from the stem of *C. pteridoides* is shown in Fig. 30. The stele is solid, more or less columnar, and is surrounded by the cortex which is composed of large, spherical, thin-walled parenchyma cells. The xylem, which lies in the center of the stele, consists of scalariform tracheids (Fig. 28, 41). According to Ford (1902) the stele is bicollateral, has endodermis and pericycle.

Vascular system. The vascular system of the sporeling has only a single vascular strand which runs throughout the whole plant body except in the laminum where the bundle branches and rebranches more or less dichotomously, and finally rejoins to form a network (Fig. 10). The venation in the cotyledon is especially simple; sometimes only a single unbranched bundle can be observed (Fig. 19, 20). No vascular strand runs through the foot between the prothallus and sporophyte. (Fig. 31).

The anatomy of the nodal region. The plant body of *Ceratopteris* consists of phytons which are joined by a short strand of vascular tissues (Fig. 11, 26, 38, 40, 41). The interconnecting vascular strand is formed through a mass of cells which is homologous with the 'foot' as a downward extension of the vascular bundle from the provascular elements in the juvenile phyton to join the phyton next below it, and is not a pre-existing axis or stem. It is well known in angiosperms that the young vascular elements originate first in younger leaves and then develop downward to connect with the older elements (Esau, 1954). The formation of the interconnecting vascular strand seems to require the pre-existing vascular elements, since no vascular strand is formed through the foot between the cotyledonary phyton and the prothallus (Fig. 31). The experimental induction of the differentiation of a vascular strand basipetally from the pre-vascular tissue of a grafted bud to join the vascular elements in the callus on which the bud was grafted has been demonstrated in *Scorzonera* by Camus (1947). In his experiment, the callus provides the pre-existing vascular elements. It is interesting that the stem would be artificially made or transformed from the basal part of the stipe by graft of a bud on the middle of the stipe; the portion of the stipe below the grafted point would be a new stem. The success of the experimental induction of the formation of the interconnecting vascular strand between two individual phytons would be strong experimental evidence for the phytonic idea. As previously mentioned, the node is the point where the interconnecting vascular bundle joins to the bundle of the next phyton just below it (Fig. 26). Fig. 27, 28 and 29 are the sections from a relatively mature or fully developed node of the sporeling of *C. pteridoides*. Fig. 32–36 are the successive serial sections from the node of the same species showing the leaf trace departing and the root trace departing. The interconnecting vascular strand can be seen more clearly if the longitudinal sections were made especially at the younger node (Fig. 38, 40, 41). In summary, a nodal region consists of a root trace, a leaf trace (sometimes two traces), an interconnecting vascular strand and a node (Fig. 26).

Shoot apex. The terminal bud or shoot apical growing point of the *Ceratopteris* sporeling is enveloped in one or two layers of ramenta (Fig. 22, 37). The internal



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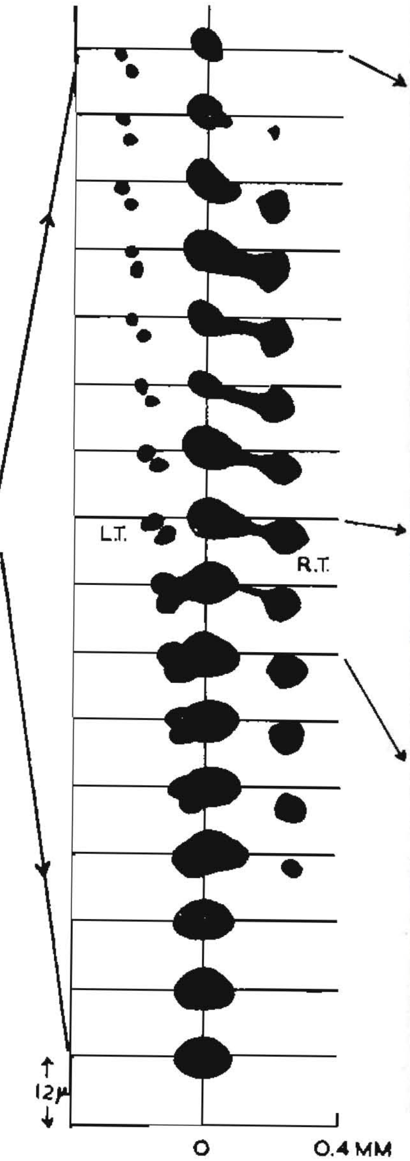

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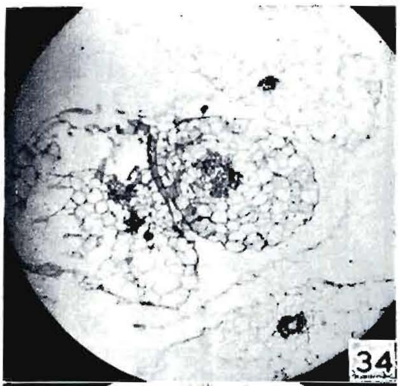

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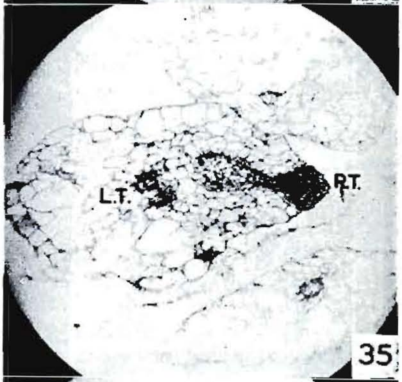

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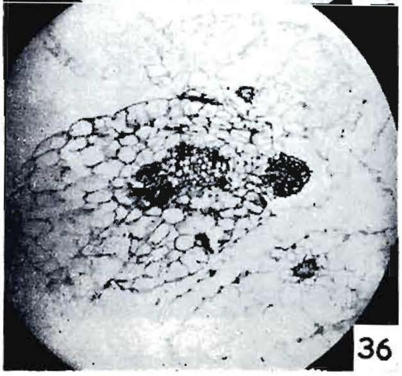

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Fig. 32-36. Nodal anatomy in *C. pteridoides* All ×45—Fig. 32. Vascular tissues from the nodal region where the sections illustrated in Fig. 33-36 were made.—Fig. 33. Serial sections (at 12 μ thick) of the nodal region depicted in Fig. 32, showing departing of leaf trace and root trace. —Fig. 34-36. Photographs of transections through the nodal region correspond to some sections shown in Fig. 33.

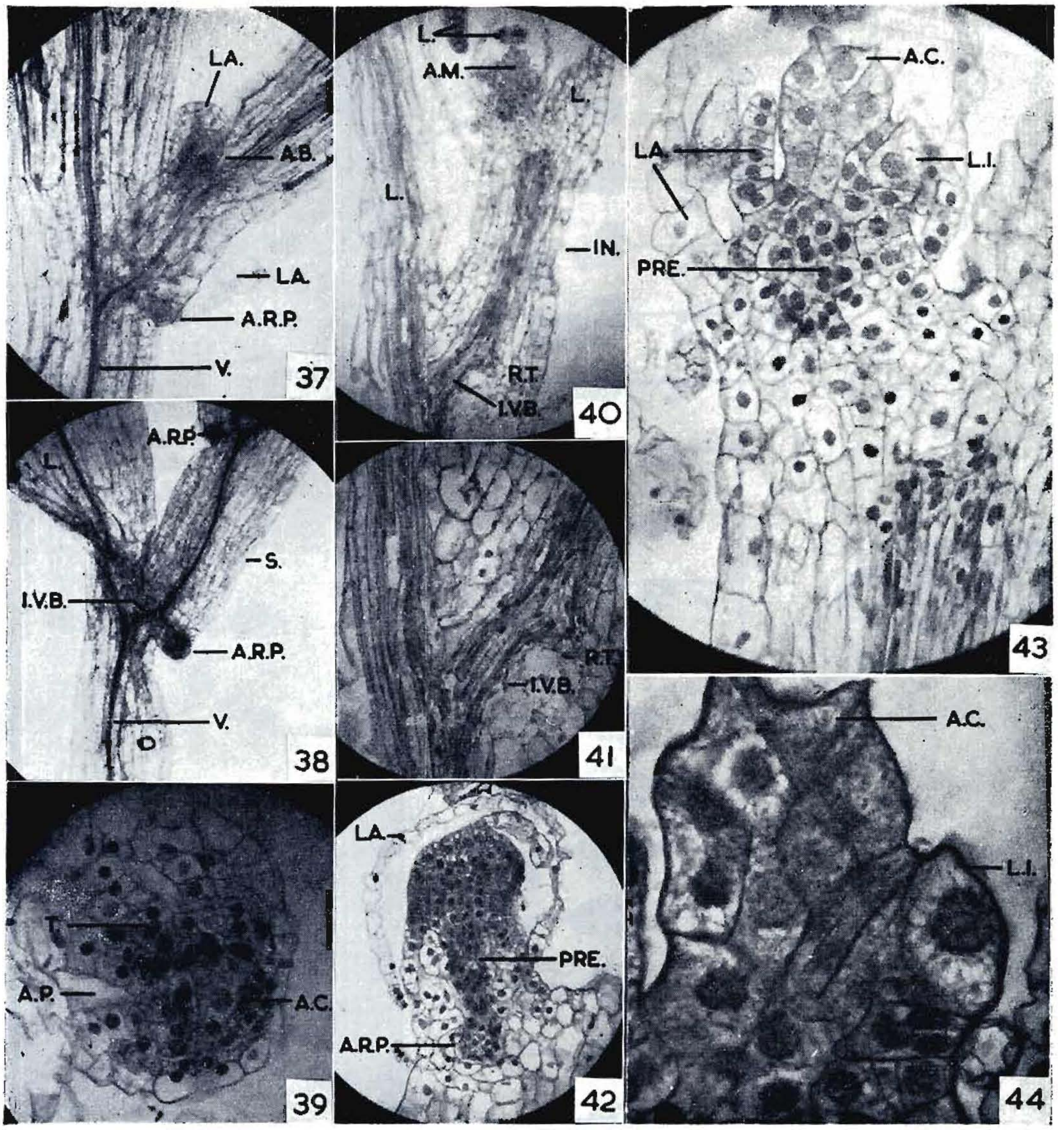

Fig. 37-44. *C. thalictroides.* A. B., apical bud or terminal bud; A. C., apical cell or apical cell or apical phyton initial cell; A. P., air passage; A. R. P., adventitious root primordium; I. V. B., interconneting vascular bundle; IN., internode; L., leaf; L. I., leaf initial; LA., ramentum; PRE., prevascular tissue; S., stem; T., trabecula; V., vascular bundle.—Fig. 37. Portion of shoot tip showing terminal bud, adventitious root primordium, ramenta and vascular system. ×15.—Fig. 38. Nodal region showing interconnecting vascular bundle and arising from adventitious root. ×15.—Fig. 39. Oblique section of a young root through the apical cell. ×210.—Fig. 40. Longitudinal section of a stem tip. ×95—Fig. 41. Nodal region showing interconnecting vascular bundle and emergence of root trace. Fig. 41 is a magnified photograph of the lower area of Fig. 40. ×100—Fig. 42. A young developing phyton of the same sporeling in Fig. 40. ×100.—Fig. 43. Shoot apical meristem and its subjacent structures. Magnified from the upper area of Fig. 40. ×200.—Fig. 44. Apical meristem of same apex in Fig. 43, section of 8 μ next to it. ×320.

structures of the shoot apex of *C. thalictroides* are shown in Fig. 43, 44, and 45. The apical meristem of the shoot is an aggregation of immature phytons and one apical phyton initial cell (Fig. 45–50). It is distinctly conical. A single apical phyton initial or shoot apical cell is located at the extreme tip of the cone (Fig. 43, 45). It has a three sided pyramidal shape with a convex base and has a large, conspicuous nucleus. The new phytons are formed one by one from this initial cell by cell division parallel to the lateral walls. The derivative is the phyton at the one-celled stage of development, and is not the stem initial as might be considered by the defender of the axial theory. The first division of the derivative or the one-celled phyton forms an anticlinal wall from which two unequal cells are formed (Fig. 47, 48). This is a phyton at the two-celled stage. The smaller inner cell, which is homologous with the foot initial of the quadrants, gives rise to a group of cells. This group of cells corresponds to the foot of the embryo and differentiates into the interconnecting vascular bundle through which it joins two adjacent phytons. The interconnecting vascular bundle is thus not a pre-existing stem, since the foot of the cotyledonary phyton never

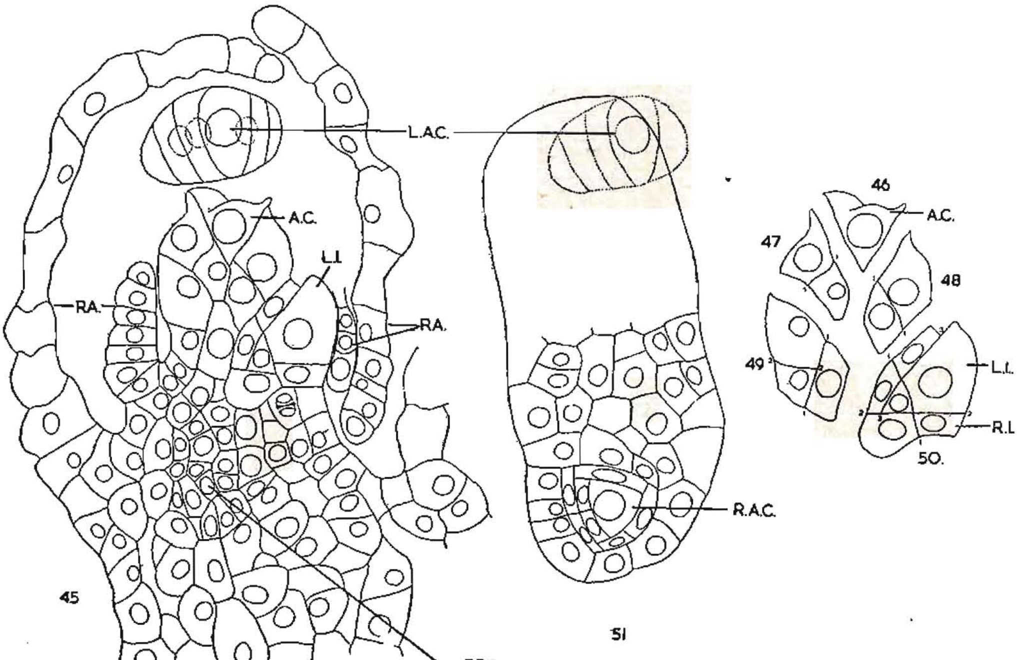

Fig. 45-51. Internal structures of apical bud of *C. thalictroides*. All ×200. A. C., apical cell of shoot or apical phyton initial cell; RA., ramentum; L. A. C., leaf apical cell; L. I., leaf initial; R. A. C., root apical cell; R. I. root initial; PRE., prevascular tissue.—Fig. 45. Medial, longitudinal section.—Fig. 46-50. Separation of apical meristem in Fig. 45 into several phytons and an apical phyton initial.—Fig. 46. Apical phyton initial.—Fig. 47-48. Two-cell phytons.—Fig. 49. Three-cell phyton.—Fig. 50. Phyton with a conspicuous leaf initial. 1-1-3-3 indicate the first three walls.—Fig. 51. Phyton with a root apical cell and leaf apical cell.

produces it. The larger, outer cell gives rise to the leaf and root. The leaf initial cell of the phyon is a large conspicuous wedge-shaped cell (Fig. 50). The root initial cell derived from the cell immediately below the leaf initial cell (Howe, 1931). There is a very close positional relationship between leaf and root. It must be emphasized that no axis or stem as such can be found in the shoot apical meristem of this fern. The internal structure of the shoot apex of *C. pteridoides*, which is essentially the same with *C. thalictroides*, is shown in Fig. 52–57 in transverse sections.

It is thought, although some workers have questioned it, that the quadrants of the leptosporangiate fern embryo are definitely related to the primary organs: the inner and outer posterior quadrants become foot and primary root respectively, and the inner and outer anterior quadrants become shoot apex and first leaf respectively (Fig. 58) (Foster and Gifford, 1959; Wardlaw, 1955). The early embryogeny of *C. thalictroides* has been studied by Kny (1875) and Mahabalé (1948). Kny thought that both the anterior quadrants participate in the formation of the leaf from which the stem arises afterward as a lateral bud. Mahabalé reported that the early embryogeny is normal, *i.e.*, it agrees with those in the *Polypodiaceae*. The embryo of *Ceratopteris* was not studied by the present authors. However, from the study of the shoot apical meristem a different opinion on the early embryogeny was obtained and it is suggested that the shoot apical meristem and the young embryo are closely homologous. This idea of homology is based on the fact that the phytons produced by both of them are exactly the same, *i.e.*, there is no difference between the cotyledonary phyton and the subsequently formed phytons. The extraordinary simplicity of the apical meristem, which consists of only a few cells, also made it possible to compare the shoot apical meristem with the embryo at the quadrant stage of embryogeny (Fig. 58). The classic and Vladesco's views of the early embryogeny in leptosporangiate ferns (cited in Wardlaw, 1955) are also illustrated in Fig. 58 for contrast. It is suggested that the apical phyton initial is closedly homologous with the zygote, and the apical meristem of the shoot with the young embryo. From this, it is further suggested that the embryo of this fern at the quadrant stage of embryogeny consists of the apical phyton initial, a two-celled cotyledonary phyton, and a one-celled first phyton (Fig. 58).

The shoot apex of *C. thalictroides* has been studied by Ford (1902), Howe (1931), and recently by Gifford (1960). The present report is the first one concerning the body constitution of this fern. Several types of shoot apical meristems known in vascular plants have been described by Wardlaw (1952). The shoot apex of *Ceratopteris*, which was not cited, probably belongs to the simplest type among all known *Tracheophyta*.

The constitution of the plant body. The present investigation clearly reveals that the plant body of *Ceratopteris* is an aggregation of phytons. The phyton is made up of leaf, stem and root. The stem of a phyton, which is morphologically the basal

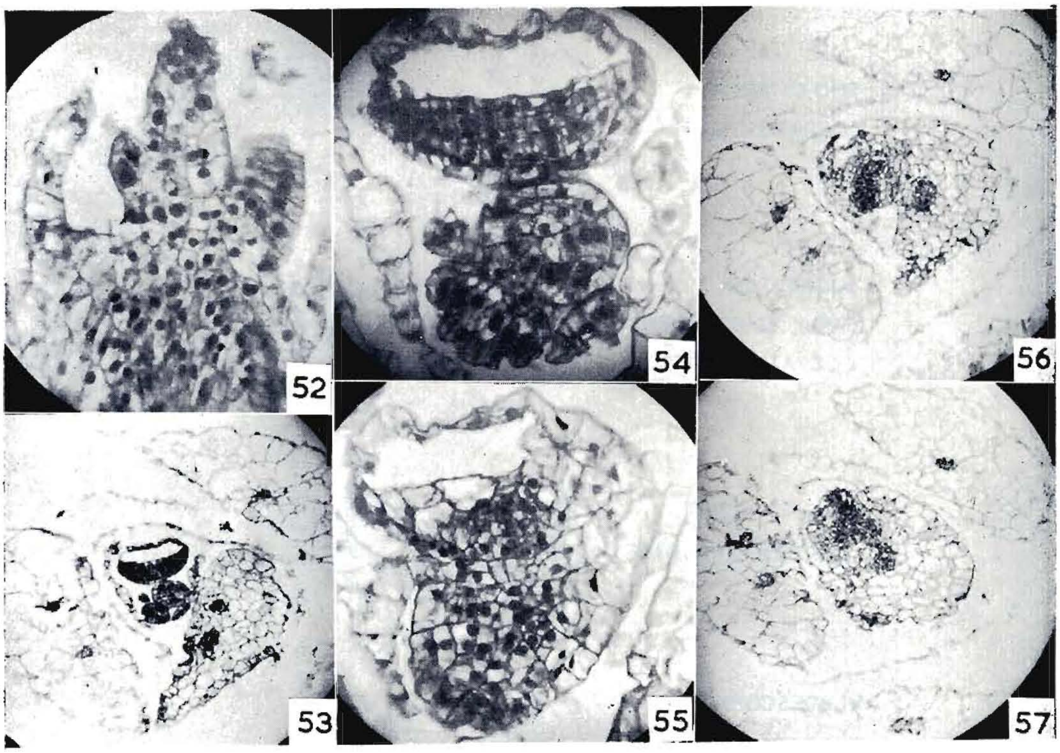

Fig. 52–57. Internal structures of shoot apex in *C. pteridoides*.—Fig. 52. Longitudinal section. ×190.—Fig. 53–57. Transections at various levels from shoot apex. The sections were cut at the following numbers of microns below the apical phyton initial: Fig. 53, 70; Fig. 54, 80; Fig. 55, 100; Fig. 56, 140; Fig. 57, 170. Magnification: Fig. 53, 56 and 57, ×50; Fig. 54 and 55, ×200.

part of the leaf, contributes as an internode to the plant body. The phytons are joined one by one with a short strand of interconnecting vascular tissues which is not a pre-existing axis or stem. The sporophyte of this fern is thus considered to be a complex organism. All these results support the phyton theory which claims that the leaf is the fundamental structure in the plant body and the stem is a secondary structure transformed from the leaf. The phytonic idea and its analogous ideas have been developed by many workers (Goethe, 1790; Gaudichaud, 1841; Schultz, 1843; Delpino, 1880; Čelakovský, 1901; Chauveaud, 1921; Majumdar, 1947). Goethe's explanation which seems to represent the common point of these ideas, is illustrated in Fig. 12. *Ceratopteris* has been pointed out as an evidence of phytonism by Čelakovský (1901). Several theories other than the phyton theory have been developed to interpret the leaf-stem relationship in *Tracheophyta* (Eames, 1936; Wardlaw, 1952). According to the axial theories (either veiw of the enation and overtopping theories), the leaf is elaborated from the pre-existing axis or stem and is merely a lateral appendage produced secondarily by the stem. Wolff's idea (1759), which is illustrated

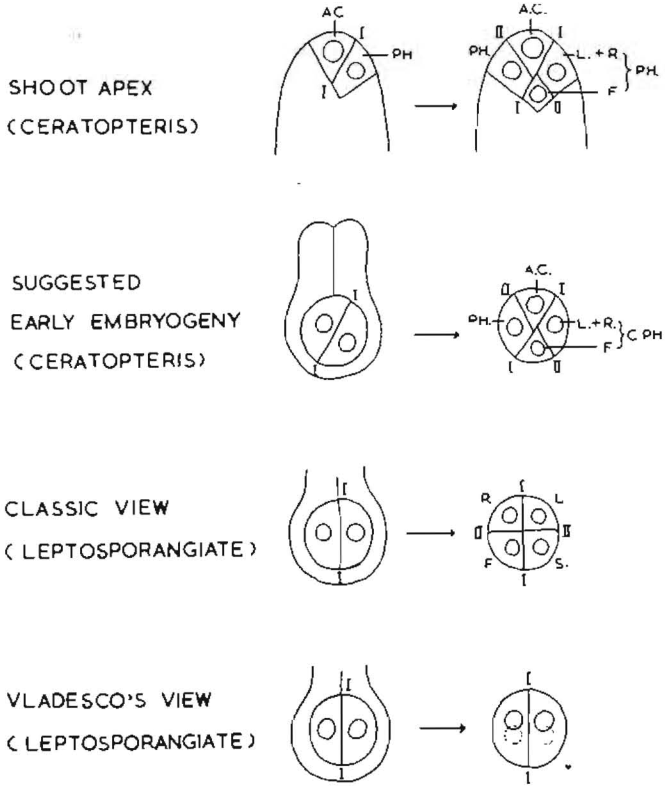

Fig. 58. Diagram showing comparison among segmentation patterns of the apical phyton initial cell and zygote in *Ceratopteris* and the other leptosporangiate ferns. A. C., apical cell or apical phyton initial cell; F., foot quadrant; L., leaf quadrant; R. root quadrant; S., stem quadrant; L. +R., quadrant which gives rise to leaf and root; PH., phyton; C. PH., cotyledonary phyton; I—I, first partition wall, or basal wall; II—II, second partition wall, or median wall.

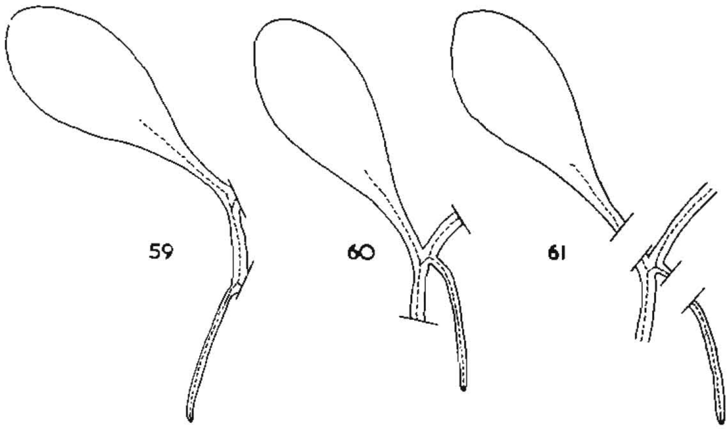

Fig. 59-61. Different methods of exision by which a sporeling is segmented.—Fig. 59. A perfect phyton with leaf, stem and root.—Fig. 60. A segment with functionless stem.—Fig. 61. Resulting parts are more or less physiologically dependent upon each other. This method is evidently unnatural as well as that of Fig. 60.

in Fig. 13, is a classic example representing the common point of these ideas. Arber has proposed the partial-shoot hypothesis (1950).

In conclusion, evidences of the phytonic constitution of the plant body in the *Ceratopteris* sporeling are listed below: 1) The phytons of a sporeling are visibly discrete; the external morphology of a nodal region shows that the boundary between two adjacent phytons is visibly clear. 2) There is a very close connection between the number of leaves and roots. 3) The roots exhibit a positional relationship with leaves. The orientation of the roots always coincide with that of the leaf in the same phyton. 4) The occurrence of the adventitious root is always slightly above the node; *i.e.*, at the base of the internode, or at the base of the stem of the phyton. 5) No pre-existing axis or stem can be recognized in the shoot apical meristem. The interconnecting vascular strand differentiated in the 'foot', and is not a pre-existing stem. 6) No physiological problem would arise, for example, in the translocation of materials, in an excised fully developed phyton (Fig. 59). If the excision is made, into stem, leaf and root (Fig. 61), each excised part is obviously physiologically dependent or incomplete. If the plant body is excised at the middle of each internode as shown in Fig. 60, translocation through the interconnecting vascular strand would be in an opposite direction, and both excised ends of the internode would become functionless.

Physiological function of the phyton. It is obvious that the young developing phytons as well as the apical phyton initial are nutritionally dependent, since they do not have chlorophyll. They must be nourished by the adult phytons. The juvenile cotyledonary phyton is fed by the prothallus. With an excised phyton culture, the factors affecting differentiation and growth of new phytons may be studied.

Environmental conditions for stem elongation. The sporelings with elongated internodes as described above were obtained under the following conditions: 1) When the sporelings were grown under the shade of the mother plants or other materials. 2) When many sporelings were closely grown together. 3) When the sporelings were cultured in Petri-dishes in the laboratory under the moderate natural diffuse light. It is concluded that the relatively low intensity of natural day light seems favorable for the internode elongation of the sporeling. Recently Laetsch and Briggs (1962) reported red, far-red photoreversible effects on internode elongation of the sporeling of a heterosporous aquatic fern, *Marsilea vestita.*

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