

# REPEATED FISSION OF STEM AND ROOT IN *MERTENSIA* *MARITIMA*—A STUDY IN ECOLOGICAL ANATOMY \*

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## INTRODUCTION

Among the many types of "abnormalities" which have been recorded in the mode of secondary thickening of the stem and root in dicotyledonous plants, none is more striking than that which involves the division of the axis into columns or strands which are externally distinct. Fission of this character is of regular occurrence chiefly in the stems of certain highly specialized tropical lianas, and in the rhizomes and roots of a small number of herbaceous perennials. The old herbalists were long ago familiar with the split rhizomes of several plants indigenous to Europe, and as early as 1849 Irmisch (9) gave a description of the method of dissection of some species of gentians. Later Jost (11) published a paper on "Die Zerklüftungen einiger Rhizome und Wurzeln," which remains the classic work on the subject, and in which he described the occurrence of fission in a number of species belonging to six genera of European herbs. Since the appearance of Jost's paper a few cases have been added to his list, but the process of fission in *Mertensia maritima*, which exhibits a degree of complexity far exceeding any of the previously described examples, and approaching that which obtains in certain lianas as described by Schenck (20), has apparently never

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\* The publication of this paper (Botanical Contribution from the Johns Hopkins University, No. 105) has been made possible through a grant from the income of the Esther Herrman Fund of the N. Y. Academy of Sciences.



received the attention which it merits. It was to supply this deficiency, and to attempt to correlate the unique anatomical features of the plant with the peculiar conditions it encounters in the shingle beaches, the habitat in which it seems to thrive best, that the present study was undertaken.

My study of *Mertensia* was begun during the summer of 1925, while working under the guidance of Professor Duncan S. Johnson at the Mount Desert Island Biological Laboratory at Bar Harbor, Maine. The investigation of the anatomical details was continued in the botanical laboratory of the Johns Hopkins University, where the writer held the James Buchanan Johnston Scholarship, and in early June, 1928, a visit was made to Mount Desert Island to observe the behavior of the plant in the field at the outset of the growing season. I desire to express my warmest gratitude to Professor Johnson for the helpful and sympathetic criticism which he has continued to give throughout the course of this work, and to him and Mr. George D. Johnson for the collection of material in the late summer of 1928, when I was unable to visit the Island.

### THE PLANT AND ITS HABITAT

The sea lungwort, *Mertensia maritima* (L.) S. F. Gray is a plant of widespread occurrence on the seacoasts of high latitudes throughout the Northern Hemisphere [Gray (6)] \*. On our Atlantic Coast it pushes down as far as Nantucket Island off the coast of Massachusetts, but is not at all frequent south of Maine, whence it ranges northward to Baffin Land and the Arctic Archipelago, and extends up the west coast of Greenland at least as far as Pröven, at 72° N. latitude [Kane (12)]. As I know it on Mt. Desert Island, Maine, where all of the material employed in the present study was collected, it is essentially a plant of shingle beaches on the exposed shores, and I am not aware of its occurrence on the rocky, but sheltered, northern coast of the island. From other sources we find references to its presence on gravelly barrier beaches and sandy beaches in Nova Scotia [Fernald (5)] and on beaches of coarse sand in the Faeroës [Ostenfeld (15)], and taxonomic works give as its habitat both sandy and rocky shores. But the shingle beach seems to be a favored habitat; thus Carey and Oliver (2) record that it is one of the local rarities of Blakeney Point, Norfolk, England, where it grows on the extensive shingle deposits.

\* Throughout this paper the italicized figures in parentheses refer to works, similarly designated, in the Bibliography.



The shingle beaches which are the habitat of *Mertensia* on Mt. Desert Island are of two forms—the fringing type, which lies in direct contact with the higher land behind the shore; and the bar or barrier type, which occurs as a ridge of shingle between the sea and the salt meadow, lagoon or the dammed mouth of a stream, as the case may be, which lies to the landward of it [see Carey and Oliver (2), Oliver (14)]. The largest and most vigorous plants grew on beaches of the bar type, in mobile shingle (Pl. I, fig. 1). A beach of this form along the western side of Bass Harbor is composed of small, rounded stones of gray shale, averaging about the size of a walnut, which shift with a rattling and grating sound as one walks across them. The shingle ridge rises steeply from the water's edge to the flat crest at about 5-6 feet above the mean high water level, whence it falls abruptly on the landward side to a salt meadow dominated by *Triglochin maritima* and *Myrica gale*, lying some 5-8 ft. below its summit. The plants of *Mertensia* grew principally on the level summit and on the seaward face of the ridge, where the lowest were several feet above the reach of the tides. In June, 1928, dead stems of the previous summer, lying undisturbed on the shingle beneath the new shoots of the season's growth, gave evidence that the higher plants on this bar had not been reached by the waves of this comparatively quiet body of water during the previous winter, but individuals lower down on the seaward face were mingled with dead algæ and the varied debris washed up by the billows. Even the plants on the summit, however, had during previous winters' storms been buried by the up-building shingle to the depth of over a foot since their establishment as seedlings.

Near by were a series of local beaches of the fringing type, lying between outcropping ledges of the rocky shore, and some of these had been stable for a number of years, during which the interstices between the stones had become filled with sand and fine gravel. The plants of these beaches were never half so large as the largest on the bar. Another shingle bar near Manset, composed of large, angular rocks intermixed with the smaller, rounded stones, stood in part above a *Triglochin* meadow and in part above a lagoon formed by the damming of a small, fresh-water stream (Pl. I, fig. 1). Here also *Mertensia* grew on the seaward face near the top of the beach, and the plants were larger than any found on the extensive reaches of fringing shingle beach near by.

The characteristics of the shingle beach as a plant habitat have been considered in several papers by Oliver and his students (8, 14). By themselves, the rounded stones washed up by the waves to form a bar or



a fringing beach would constitute a very poor habitat for vascular plants of any sort, but in the beaches on which *Mertensia* is established all but the most superficial layers of shingle contain a greater or less accumulation of soil. This consists of sand and fine gravel, either washed up by the waves or ground off the larger stones, calcareous matter derived from shells which are washed into the shingle and usually ground into fine pieces by the attrition of the larger stones, and finally of a quite considerable amount of organic material derived from flotsam of every conceivable sort deposited on the beach (Pl. II, fig. 4). The latter is made up principally of seaweeds, but contains also much wood and a certain amount of animal remains. When the beach is of the fringing type, its soil content may be augmented by material eroded from the land behind it, but in the case of bars, practically everything must be derived from the wash of the sea. Carey and Oliver (2) and Hill and Hanley (8) have considered the water content of shingle beaches. They record that these always contain an abundance of fresh soil water, even when meadows and woods inland to them are parched from a prolonged drought. Although, in certain cases at least, the water supply of a fringing beach may be augmented by run-off and seepage from the land, or by capillary rise from a fresh water table beneath it, it is evident that the shingle bar, standing as it does above the surface of the land or water behind it, is entirely cut off from such sources of moisture. The most obvious manner in which it receives fresh water is by rainfall and dew formation, but apparently these sources are not sufficient in all cases to account for the liberal supply usually present. Oliver (14) makes the interesting suggestion that fresh water may be added to the superficial layers of the beach by distillation from the sea water which penetrates beneath it, or, as he terms it, by "internal dew formation."

When a seedling of *Mertensia*, surviving the great odds against establishment in the inhospitable habitat we have just described, becomes firmly rooted, the hypocotyl and the upper portion of the primary root thicken into a fleshy, spindle-shaped tap-root, while a rosette of leaves develops above the cotyledonary node (Pl. III, fig. 5). In the second summer of the plant's existence one or, more often, several aerial flowering shoots grow out from the axillary buds at the crown of the tap-root and lie along the surface of the shingle. These aerial shoots, which are usually unbranched, die back to the tap-root in the fall, but in each succeeding spring a still larger number of more vigorous shoots grow out from the buds at the crown of the perennating hypocotyl, and lie on the shingle radiating in all directions from the original point of establish-



ment of the plant (Pl. I, fig. 1; Pl. II, fig. 3). The foliage of these decumbent shoots stands above the stems on short, ill-defined petioles; the ovate, obovate or spatulate leaves are covered with a thick waxy bloom, which imparts a striking glaucous color to the low and spreading mass of herbage each large plant produces; the delicate blue flowers, produced in July and August, are borne on short, ascending peduncles. The number of buds at the crown increases from year to year, until in a few seasons they form a thick, swollen mass, some of which each year give rise to the current flowering shoots. Meanwhile the tap-root has thickened considerably, and has become divided, in the manner which is described in detail below, into a large number of anastomosing strands (Pl. III, fig. 6; Pl. VII, fig. 13; Pl. VIII, fig. 15), each of which is divided anew at the outset of every growing season. The root system consists of a rather restricted number of thick, fleshy roots and their finer laterals (Pl. I, fig. 2). The lateral roots run horizontally through the shingle for considerable distances and one was traced for a length of 90 centimeters from the tap-root. They thicken and become split longitudinally in a fashion very similar to the tap-root.

Still more interesting and complex are the life history and structure of a plant which grows in a shingle beach the level of which has been raised since the establishment of the individual. In the spring of 1928, I found plants which in three winters had been buried to the depth of 40 cm. (Pl. IV, fig. 7). All of the largest plants which I found on Mt. Desert Island had been buried more or less deeply by accretions of shingle since their germination. The violent surf which shifts the shingle at the levels where *Mertensia* is established is usually the product of the winter storms. In the following spring some of the buds at the crown of the tap-root (if it is a plant which has been buried for the first time) break their dormancy and push up through the overlying debris of shingle, and the decaying flotsam and jetsam which has been incorporated with it, as slender, etiolated shoots, much contorted from their sinuous passage between the stones (Pl. II, fig. 4; Pl. VII, fig. 14). Having emerged from the shingle, they continue to grow over it as green, leafy shoots of normal appearance. While the aerial portions of such stems die off in winter, the buried portions, differing greatly from the former in internal organization, survive the cold months and constitute an addition to the perennating portion of the plant. In the succeeding spring the lateral buds of the subterranean length of the shoot give rise to the flowering shoots, while the buried axis becomes dissected into strands in a manner somewhat similar to the hypocotyl and roots. Other



shoots may still arise from the crown of the tap-root, even at a depth of 40 cm. beneath the surface. At the beginning of the second season's activity each strand is again divided into several strands of a higher order. The dormant buds at the nodes increase in number until the groups of them form great swellings, at which the strands, separate from each other in the intervening stretches of the stem, are bound together by vascular anastomoses.

Thus the subterranean, perennating portion of a large, old plant becomes a thing of bewildering complexity. Such a plant, found growing on the bar at Bass Harbor in August, 1925, was the most impressive specimen which I unearthed (Pl. VIII, fig. 16). The lowest mass of dormant buds, 30 cm. beneath the surface, indicated the crown of the tap-root and the original level of the shingle, which had been built up 30 cm. since the establishment of the seedling. The tap-root had disintegrated into a large number of rather slender, anastomosing strands. From this arose lateral roots, the largest of which had become divided into a thick, cable-like bundle of spirally twisted strands (Pl. V, fig. 9). Because of the great difficulty of digging in the shifting shingle, which to one's great exasperation rolled into the excavation almost as rapidly as it could be removed, it was not possible to expose the whole root system of the plant. From the crown of the tap-root, which was 7 cm. in diameter, the dissected perennial stems arose in a tangled cluster, which expanded to twice that diameter 30 cm. higher up, at the surface of the beach. Shells and small, rounded stones were impacted in the mass of stranded stems. From the mode of branching of these stems it seems probable that the shingle had been piled up over the plant during several different winters, and not all in a single period of dormancy. From the top of this inverted cone of perennial branches arose the annual flowering stems of the season's growth. There were 117 of them which, lying prone over the shingle, completely covered it over a circle 180 cm. in diameter. This plant was at least four years old, and probably not more than five, although the exact age of such a large plant is not so easy to determine as that of a younger specimen. Another large plant, growing near by, consisted of 266 flowering stems, which covered a circle 210 cm. in diameter.

Although the formation of such an extensive but still subterranean superstructure above the tap-root provides a larger base for the support of a great quantity of the annual flowering shoots, plants which have not been deeply buried produce a surprisingly large number of them. Thus a specimen found near Manset, which consisted of 260 flowering



stems, covering a circle of 120 cm. in diameter in early June, while they were still elongating vigorously, had been buried to a depth of only 8 cm. (this is the plant shown in Pl. I, fig. 2; Pl. II, fig. 3). The flattened hypocotyl of this plant was 7 cm. by 4 cm. in diameter. On the other hand, plants growing in quieter shingle, which had not been built up at all since their establishment, but had been filled in with sand and finer gravel, in my experience always bore a considerably smaller number of flowering shoots.

Plants of the shingle beach are subjected not only to burial by the building up of the shingle, but frequently the process is reversed and the waves, lashed up by the winter storms, wash away the stones which surround them. A plant of *Mertensia* which since its establishment had not been covered by the upbuilding of the beach would probably succumb to any considerable exposure through the removal of the surrounding shingle. I have found no actual instance of the exposure of such a plant, but there is no indication that the partially uncovered roots would regenerate shoots and so perpetuate the individual. On the other hand, a plant which has previously been buried, and has formed a superstructure of perennating shoots above the tap-root, is well fitted to survive a subsequent uncovering, at least as far as the crown. All of the cauline portion of the plant is provided with numerous dormant buds and, when the more apical of these have been destroyed, those basally situated grow out to form the flowering shoots of the following season (Pl. IV, fig. 8).

Although, except for summer storms of unusual severity, *Mertensia* does not come into contact with salt water during its growing season, the young shoots are not injured when both they and the roots beneath them are subjected to a drenching of salt-water. Carey and Oliver (2) point out that the green shoots of the majority of the species commonly found on shingle in the British Isles suffer greatly from the contact of sea water, though a few others, such as *Glaucium luteum*, are not injured by it.

### THE SEEDLING

In 1928, seedlings were first found on June 3. Most of them had not yet produced any leaves above the cotyledons, and the germination of the seeds had evidently been quite recent. The cotyledons are epigaeous, as is general in the Boraginaceæ [Jodin (10)]. They are spatulate in outline, about 25 mm. long by 5 mm. broad in vigorous seedlings, and borne at the end of a usually slender hypocotyl, which narrows abruptly at the base, where it joins the thread-like primary root, from which



few lateral rootlets arise. The establishment of the seedlings among the loose stones of the shingle beach is fraught with great difficulty, and the early life of the plant is indeed precarious. The seeds ripen at the end of the summer. During the winter those that are not washed completely away are mixed by the waves among the superficial layers of the shingle, and many are no doubt very deeply buried. Those shed so high on the beach that they escape the winter's waves may fall or be washed by the rain deep into the interstices of the shingle. One way or another, the advent of spring finds numbers of them at a considerable distance from the surface, and indeed at the very surface on most parts of the beach they would find little but rounded stones in which to strike root.

The dimness or absence of light from the crevices in which they start their growth produces in these seedlings the typical aspect of etiolation, with small cotyledons, short root and an enormously elongated hypocotyl. Many germinate beneath stones and produce a long, twisted, exceedingly slender hypocotyl which never succeeds in pushing into the light, and on digging in favorable localities one finds many more, hopelessly buried beneath the surface of a beach that has been raised during the past winter. The longest hypocotyl measured was 125 mm. in length, although only about 0.75 mm. in diameter. The average length of nineteen others selected at random was 81 mm. and of these six were over 100 mm. long. Jodin states of the European Boraginaceæ, of which he studied numerous species, that the hypocotyl is almost always more than 15 mm. and rarely so much as 50 mm. long. The hypocotyls of these light-starved seedlings of *Mertensia* are so delicate that it is almost impossible to handle them without their breaking (see Pl. VI, fig. 12). That the long hypocotyl so commonly found is an expression of the environmental conditions under which germination occurs, rather than of the genetic constitution of the plant, is attested by the fact that the most advanced seedlings have the shortest hypocotyls. Thus the most advanced seedling found on June 3 had a hypocotyl only 37 mm. long, while the primary root measured 45 mm. The production of long, slender hypocotyls in response to environmental conditions is apparently a general characteristic of plants growing in the shingle.

A seedling arising from a larger seed containing a greater reserve of food would experience less difficulty in striking root and reaching the light, but the seeds of *Mertensia*, as is characteristic of the more familiar members of its family, are small, and many of the delicate spindling seedlings which issue from them exhaust all of their reserves in an effort to reach the light, only to perish because they have not at the same time



been able to produce an efficient root system in the gravelly interstices of the shingle. In this respect *Mertensia* is very poorly adapted to its environment. In the afternoon of a bright day one finds many seedlings lying limp and dying against the stones between which they have pushed. The mortality of the seedlings is enormous, and when one adds to this the number of seeds washed away or deeply buried by the waves, it can readily be understood why the plants of *Mertensia* are so scattered, and rarely form a close stand on the beach (Pl. I, fig. 1).

Beneath the cotyledons the stele of the hypocotyl contains two collateral bundles with a central pith. The transition of the stele to the radical type takes place in the upper portion of the hypocotyl, and the pith has usually disappeared at about one-quarter the length of the hypocotyl below the cotyledons. The lower portion of the hypocotyl and the primary root are exarch and diarch. The xylem rays, each of which consists of usually two or three elements of protoxylem and one of metaxylem, meet in the center, and so a xylem plate with two poles is formed. Although the number of elements in the rays is accordingly very small, additional metaxylem elements had differentiated beside the rays even in the youngest seedlings examined. In the upper portion of the hypocotyl the stele is limited by an endodermis of the cauline type, with a very narrow Casparian band (Fig. 23) while in its lower portion, as in the root, the Casparian band is broad and covers almost the entire radial wall of the endodermal cell. The lateral roots possess the same primary stelar structure as the primary root. The anatomy of the seedling of *Mertensia* conforms closely to the general Boraginaceous type as described by Jodin.

## ANATOMY AND EARLY FISSION OF THE HYPOCOTYL AND ROOT

Soon after the commencement of secondary thickening in the hypocotyl of the seedling, a phellogen arises in the outermost layer of the pericycle. When this occurs, it can be demonstrated that the endodermis has gone over into the "secondary stage," as characterized by Priestley and North (19). The walls, in addition to the Casparian strip, stain yellow instead of blue with chloriodide of zinc, and persist as a very delicate membrane after the treatment of sections with concentrated sulfuric acid. The activity of the phellogen in the hypocotyl and root is limited, and at the time the development of the periderm is completed it consists of usually two or three layers of cork, and one or two of phelloderm, separated by a single, inactive phellogen cell. With the formation of the periderm, the



primary cortex dies and is sloughed off. The secondary xylem consists only of tracheæ and unligified parenchyma. The vessels are reticulately thickened (Fig. 7), the pits are simple, and the ends of the vessel segments are completely open. The parenchyma cells, when examined in radial sections, lie in well-defined horizontal series, for each one retains the length of the cambial cell from which it was derived, and the end walls maintain a regular alignment. The individual segments of the vessels, where these occur, fall into the series of longitudinally elongated parenchyma cells. The secondary phloem consists of sieve-tubes, which occur together in little groups of usually three to five, although many are found singly, their companion cells and parenchyma indistinguishable from that of the xylem. The sieve-plates, which fall into line with the ends of the parenchyma cells of the same series in which the sieve-tube lies, are transverse. The walls of the sieve-tubes are slightly thickened, so that in section they stand out from the surrounding parenchyma.

Coincident with the increase in diameter of the organ, the parenchyma cells of the outer portion of the secondary cortex become tangentially elongated and divide by radial walls. Transverse walls are also formed at this time, and so the alignment of cells, so distinct in both transverse and radial sections of the younger portions of the phloem, is destroyed. The sieve-tubes about half-way across the secondary cortex from the cambium have by the end of August become clogged by the formation of thick pads of callose across their sieve-plates.

The distribution of these elements of xylem and phloem, which we have just described, deserves consideration. Opposite the protoxylem points of the diarch lower portion of the hypocotyl and of the root are formed two broad rays consisting solely of parenchyma cells of the type already described, and extending across the cambium to the periderm. These rays correspond in position with the primary medullary rays typical of woody roots, but to call them such in this case might prove misleading, because the cells of which they are composed differ fundamentally from those we generally associate with medullary rays. Alternating with these rays, two sectors of vessels and sieve-tubes are produced. As the organ thickens, these fork repeatedly, leaving gaps which are occupied by secondary rays of parenchyma. These rays of parenchyma are usually broad in comparison with the rays in which the vessels are distributed, and occasionally new wedges of vessels are formed in them, and these accordingly have no contact at their inner ends with the central mass of xylem (Fig. 2). The vessels in each wedge are separated by parenchyma cells similar to those of the parenchyma rays (Fig. 1). The groups of sieve-tubes lie imbedded



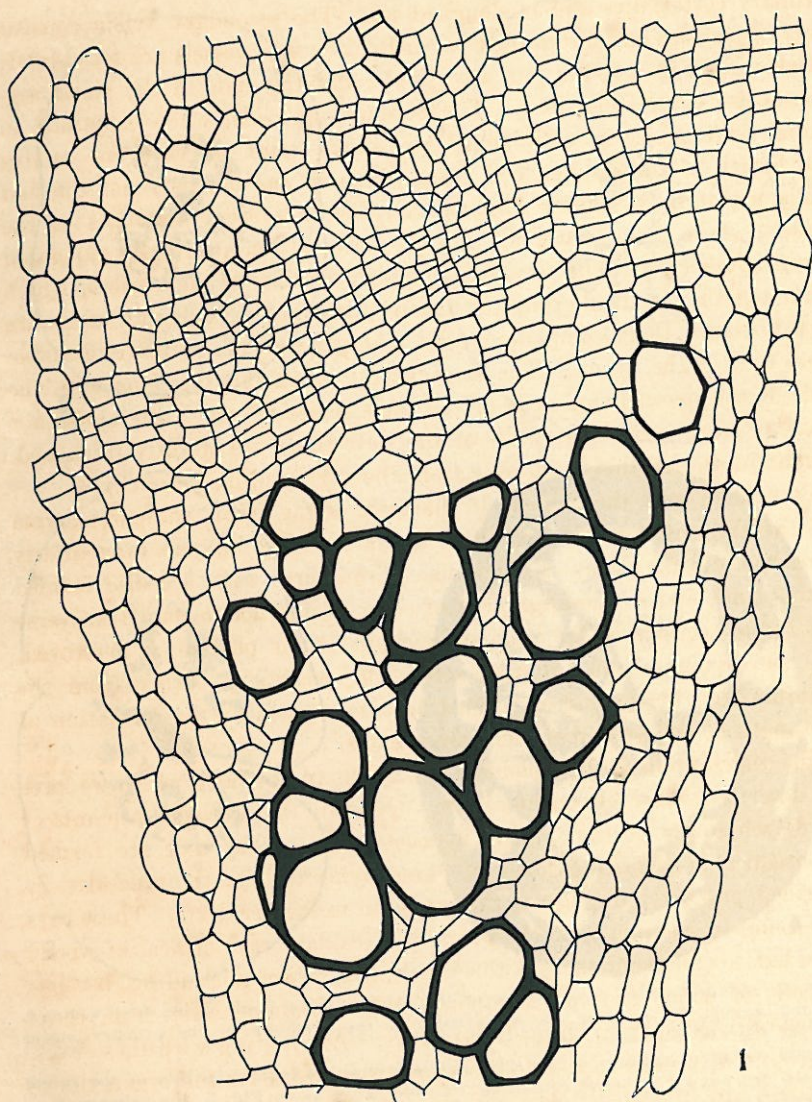


FIG. 1.—Cross-section of the tap-root of a plant about three months old, collected on August 19, showing a portion of a single wedge of vessels and sieve-tubes, with the intervening cambium and a portion of the parenchyma rays on either side. Notice the greater activity of the cambium in the wedge than on either side of it. (Camera lucida, approximately  $\times 260$ .)

in parenchyma opposite the ends of the wedges of vessels and, when the latter fork, the masses of sieve-tubes also fork. This general sectorial



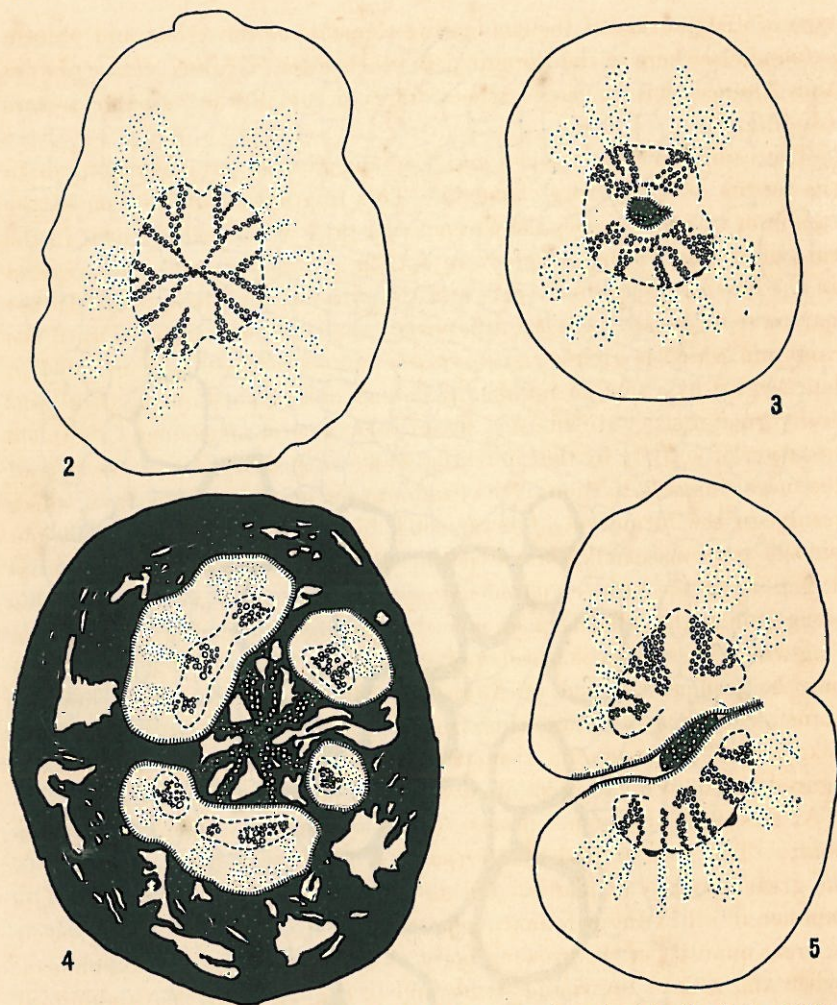


FIG. 2.—Diagrammatic cross-section of the tap-root of a plant in its first summer, collected August 19, showing the embayment of the cambium in the primary xylem rays (at top and bottom of figure,  $\times 6$ ).

FIG. 3.—Another tap-root of the same age in which the central portion of the xylem has been cut out by periderm formation (in this figure as in Fig. 5, the primary rays lie across the page,  $\times 6$ ).

FIG. 4.—Cross-section of the tap-root of a 1-year-old plant, collected June 7, showing its dissection at this level into four strands ( $\times 12$ ).

FIG. 5.—A strong lateral root of a plant in its second summer, collected August 19, which has progressed farther in its late summer fission than the tap-root in Fig. 3 ( $\times 6$ ).

In all the figures cambium is indicated by broken line, periderm (where it occurs on interior surfaces only) by hatching, the approximate distribution of vessels by open circles, of sieve-tubes by coarse stippling. Living tissues shown in white, dead tissues in black. (All figures from camera lucida sketches.)



type of distribution of the conducting elements of the xylem and phloem is found elsewhere in the Boraginaceæ in *Anchusa*, *Alkanna*, *Heliotropium* and *Nonnea*, but in these genera fibres occur in the vascular sectors (Jodin).

The cambium is much less active in the rays of parenchyma than in the sectors of conducting elements. This retardation of division of the cambium where it crosses the parenchyma rays, while quite evident in the case of the narrower secondary rays (Fig. 1), is extremely pronounced in the case of the primary rays and the broader secondary rays. In the narrower secondary rays the difference in activity, as compared with the cambium which is giving rise to vessels and sieve-tubes, is manifested in late August by a smaller number of immature segments and by their generally greater size. In the very broad rays there is sometimes a complete cessation of activity by the cambium, which then disappears. Because of the more sluggish division of the cambium in the parenchyma rays, which results in the formation of fewer cells, the cells in both the xylem and phloem portions of these rays become distinctly elongated in the radial direction, in the broader parenchyma rays enormously so. Despite this elongation of the cells, deep embayments are often formed in the cambium ring where it crosses the broader rays (Figs. 2 and 3). Such a condition may be seen at the end of August in tap-roots from 6 to 8 mm. in diameter, with a cambium ring from 2.5 to 3 mm. across. The disappearance of the cambium from the parenchyma rays is described and figured by Jodin for the root of *Symphytum officinale*.

At this point it becomes necessary to discuss the storage of food in the plant. The reserve food of *Mertensia* is fat, rather than starch, as in the great majority of plants. Oil globules are very abundant in the late summer in all of the perennating portions, and in the spring they occur in great quantity at the growing point of the shoot, in the cortex, phloem, xylem and pith of the young stems, and in the region of the cambium of the new strands formed by the dissection of the older, buried organs. Small globules of oil occur even in the chloroplasts in the leaves. On the other hand, starch is regularly present only in the active sieve-tubes of stem and root, and in the cells of the starch sheath of the young shoot until the Casparian strips are differentiated in them. The distribution of fat in the tap-root presents several points of interest. In late August it was found that oil globules were abundant in and about the cambium, in the parenchyma of the vascular wedges and in that portion of the phloem containing functional sieve-tubes. At the same time, the globules were rare in the parenchyma rays, being almost absent from the centers



of the broader ones, and very sparse in the outer secondary cortex. The relative paucity of food reserves in the broader parenchyma rays is apparently correlated with the inactivity of the cambium where it crosses them.

In the more vigorous plants the tap-root may undergo fission during the first summer of the plant's life, and some of the most vigorous lateral roots become divided when they are still but a few months old. This late summer fission is by no means an invariable occurrence, and does not materially affect the form of the fission in the following spring, which is

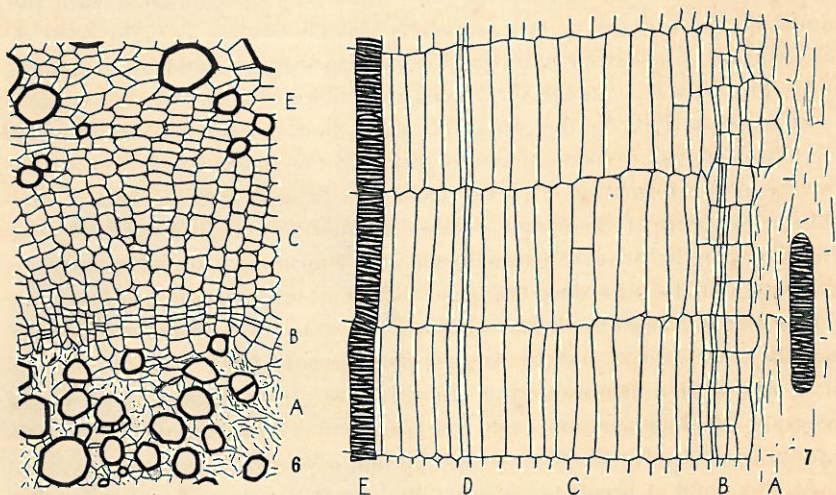


FIG. 6.—Enlargement of a region in the center of Fig. 3, showing, from bottom to top, the broken-down central xylem (A), the internal-periderm (B), the dilatation parenchyma (C), and the intact secondary xylem (E). (Camera lucida,  $\times 100$ .)

FIG. 7.—Longitudinal section through the same root at a nearby level, at which the cambium (D) is still distinguishable (Free hand,  $\times 115$ ).

of universal occurrence. The first indication of instability at the center of the root is the dilatation of the parenchyma cells, often as a pronounced radial stretching by which the elements of the protoxylem are displaced or even occluded, and the primary structure of the xylem rendered unrecognizable. At the end of August, tap-roots were found in which the central portion of the stele, including protoxylem, metaxylem and a considerable portion of secondary xylem, had been cut out by a periderm, and its cells had degenerated (Fig. 3). The origin of this periderm could not be followed in any of the material available to me. Several layers of parenchyma cells, resembling those formed from the normal cambium



ring, had been produced between the periderm and the intact xylem, apparently by a cambium of limited activity (Figs. 6 and 7). At a higher level of the same tap-root, the cambium, which first had become deeply embayed across the center of the two primary parenchyma rays, had been produced inward along the edges of these rays until it joined the newly formed central cambium, and by this means each of the two portions into which the xylem had been split was surrounded by a complete ring of cambium. The central cavity, formed through the degeneration of the xylem, had broadened laterally along the primary parenchyma rays.

Fig. 5 shows a root in which the central cavity has become confluent on one side with a furrow progressing inward along the degenerating primary ray, and the organ is almost split in half. In the root shown in the figure, unlike the tap-root just described, an active cambium could not be traced completely across the inner faces of the two divisions of the xylem. In the following spring, by the commencement of what we shall term the "normal" fission, to distinguish it from this fission of sporadic occurrence now under discussion, tap-roots are found which have become divided locally into two strands. Because this "sporadic" fission is of irregular occurrence both in respect to time and to individuals, and but a small proportion of my yearling plants collected in late August exhibited it, it was not found possible to work out its origin as thoroughly as might be desired. It is important as an illustration of how strong the tendency to cut away nonfunctional tissues has become in the plant, rather than an aid to the understanding of the "normal" fission about to be described.

The behavior of *Mertensia* during the outset of the growing season was studied during a visit to Mt. Desert Island covering the first two weeks of June, 1928, when both field and microscopic observations were made, and liberal collections of material were gathered for subsequent examination in the laboratory. At the beginning of June, the vegetation on the Island, surrounded as it is by the cold waters of the Gulf of Maine, was still in the first flush of its vernal activity, with trees burgeoning and the spring flowers in bloom. On the seashore the young shoots of *Mertensia* were just sprouting up through the shingle, and they made great progress during the fortnight which followed.

At this time the cambium in the vascular wedges shows great activity, and the numerous thin-walled cells of which it is composed crumple in hand sections into a conspicuous, darkly-staining band. The many vessels formed at this time have very wide lumina, and so contrast sharply



with the narrow tracheæ formed in the preceding autumn (Fig. 24).<sup>\*</sup> The cambium across the broader parenchyma rays is completely inactive and, because of this strict localization of growth in thickness, strains arise which result in the formation of large rents in the parenchymatous tissue of both xylem and phloem (Fig. 4) and the root has a shrunken appearance as seen from the exterior (Pl. III, fig. 5). This tissue is either already dead, or destined soon to become so. At about this time the youngest xylem and phloem is cut off from the older, inactive or dead tissue which surrounds it. The newly formed portion of a single wedge of vessels and sieve-tubes may be cut out to form a strand all by itself, or several such wedges, separated by narrow parenchyma rays, may be united in a single strand (Fig. 4). Mature parenchyma cells, lying between the narrow, scattered tracheæ which terminated each wedge of vessels at the cessation of growth in the preceding fall, become meristematic and divide very actively by tangential walls, forming a typical dilatation parenchyma. On the outer side of the future strand a stratum of mature phloem parenchyma cells, formed toward the close of the previous growing season, divides in a similar manner, but not quite so actively. Along the edges of the parenchyma rays which limit the active cambium, a row of the radially elongated cells divide by radially directed walls. These rows of cells dividing radially and tangentially are joined by others dividing in oblique planes, and so the newly formed portion of each wedge of vessels and sieve-tubes, or of a group of adjacent ones, is completely surrounded by a band of actively dividing cells.

After the band of meristematic cells has arisen, certain changes become evident in a layer of parenchyma cells, usually one cell thick, but locally two, lying to the exterior of it. The walls of these cells thicken slightly and become suberized, and numerous oil globules, which stain bright red with alkannin, lie against them, both inside and outside their lumina (Fig. 26). A phellogen arises just within this suberized layer (Fig. 25). Its activity is limited, and about two or three layers of cork and one or two of phelloderm are formed, as in the case of the primary phellogen which arises beneath the endodermis. When the intraxylary meristem has produced about eight or ten layers of cells, the true cambium is produced around the edges of the group of vessels, and thence across the newly formed dilatation parenchyma (Fig. 25). Either the newly formed portion of a single wedge of vessels may be surrounded by a cambium ring

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<sup>\*</sup> The method of fission of the root so closely resembles that of the stem that the same set of figures has been used to illustrate both.



in this manner, or several together may be enclosed by the same cambium ring. A single strand of living tissue may contain one or more cambium rings, just as it may enclose the newly formed portions of a variable number of vascular wedges (Fig. 4).

In this manner all of the newly formed xylem and phloem is cut off by periderm from the older, dying tissue. Just as the dilatation parenchyma from which both phellogen and cambium is organized arises between the narrow autumn-formed vessels of the xylem, and preserves the outer ones in the strand of living tissue, so the periderm arises among the latest formed of the previous year's sieve-tubes, and a certain number of them with their surrounding parenchyma are thereby incorporated in the new strand. These old sieve-tubes may be clearly distinguished from those just formed by the thick pads of callose which cover their sieve-plates. Their lumina, as those of most of the sieve-tubes in the older, abandoned portion of the phloem, have been more or less completely occluded by the dilatation of the neighboring parenchyma cells, and accordingly are difficult to recognize in cross-sections. The tissues exterior to the new strands have by this time been entirely depleted of the oil globules previously stored in them. Only in the proximity of the extremely active cambium is an abundance of fat found in the tap-root at this season.

During the course of the summer the tissues thus cut off by the periderm decay away and the manner in which the root has been dissected is revealed externally. By the isolation and disintegration of the primary parenchyma rays, which, as we have seen, may have taken place during the late summer of the plant's first growing season, the tap-root has fallen into two major halves running the greater portion of its length. The plane of this primary separation was accordingly determined by the orientation of the protoxylem rays. The torsion of the tap-root obscures this division, and in some plants occasional strands, representing vascular strands which had cut obliquely across the primary parenchyma rays, bind together the two divisions of the tap-root. The lateral roots, which originate opposite the protoxylem rays, lie in the plane of this separation. Since the primary parenchyma rays of these are vertical, they have become divided, usually into two, in the same plane as the tap-root. One longitudinal half of each strong lateral root then joins each half of the tap-root, and forms a further connecting link between the two portions. Finally, each of the two primary divisions has become a network of anastomosing strands, each of which is free from the others for relatively short distances only. An idea of how rapidly the appearance of the cross-section of the tap-root may change may be gained by the comparison of



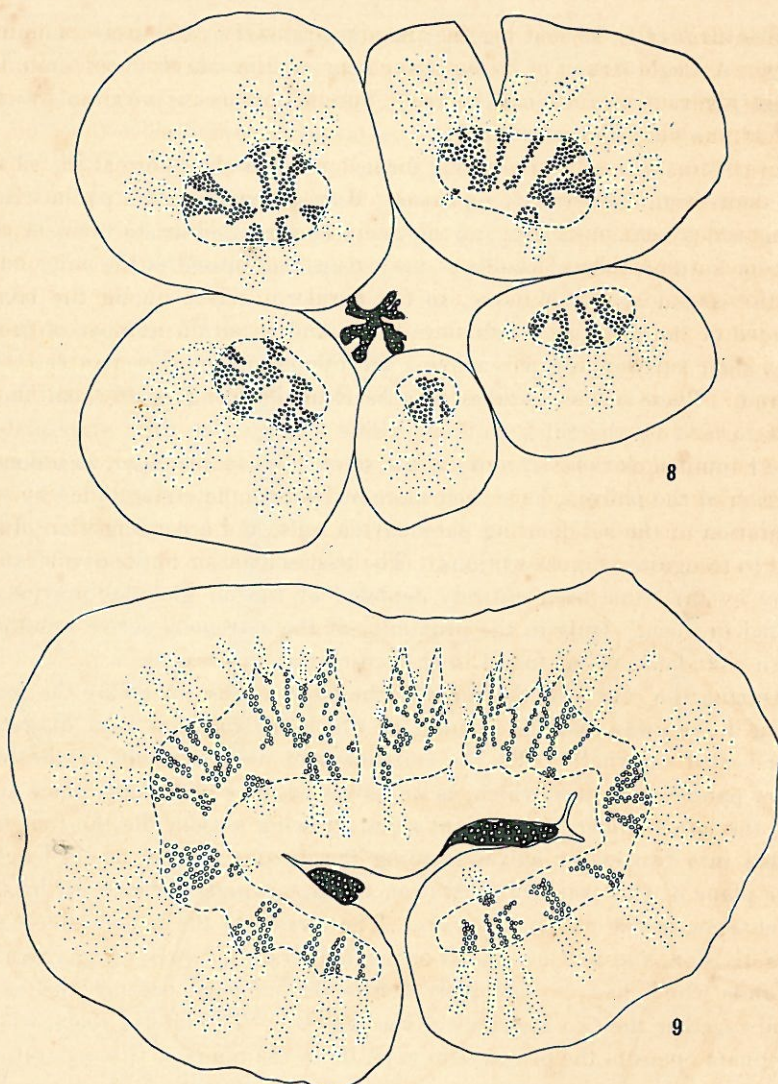


FIG. 8.—Cross-section of the tap-root shown in Pl. VII, fig. 13, collected August 19 of the second summer of the plant's life ( $\times 6$ ).

FIG. 9.—The same root about 1 cm. lower down ( $\times 6$ ). The symbols are the same as in Figs. 2-5. (Both figures from camera lucida sketches.)

Fig. 8 with Fig. 9, which represent cross-sections of the root shown in Pl. VII, fig. 13, at levels one centimeter apart. At the level of Fig. 9 the root was flattened out between two stones, the pressure of which was perhaps responsible for its failure to divide in the normal way.



The first cells formed by the arc of intraxylary cambium are parenchyma cells of the type already familiar in the unsplit root. In the more vigorous strands new vascular bundles are soon initiated by this cambium, which forms vessels on its concave face and sieve tubes on its convex face. The orientation of these bundles is then normal in respect to each particular strand, but inverted when considered in relation to the primary cambium ring of the unsplit organ. Thus the new strand becomes a radial but decidedly eccentric structure. In the case of the weaker strands, new bundles are not always initiated by the arc of intraxylary cambium, which during its limited period of activity continues to cut off parenchyma cells alone. In either case a much greater thickness of cells is formed toward the outside of the root than toward the inside (Fig. 8).

The subsequent fissions of each strand, the origin of which we have just traced, involve no new principle. Toward the end of the growing season at the outset of which they were formed, the central portion of the very strongest strands, which attain the diameter of an undivided tap-

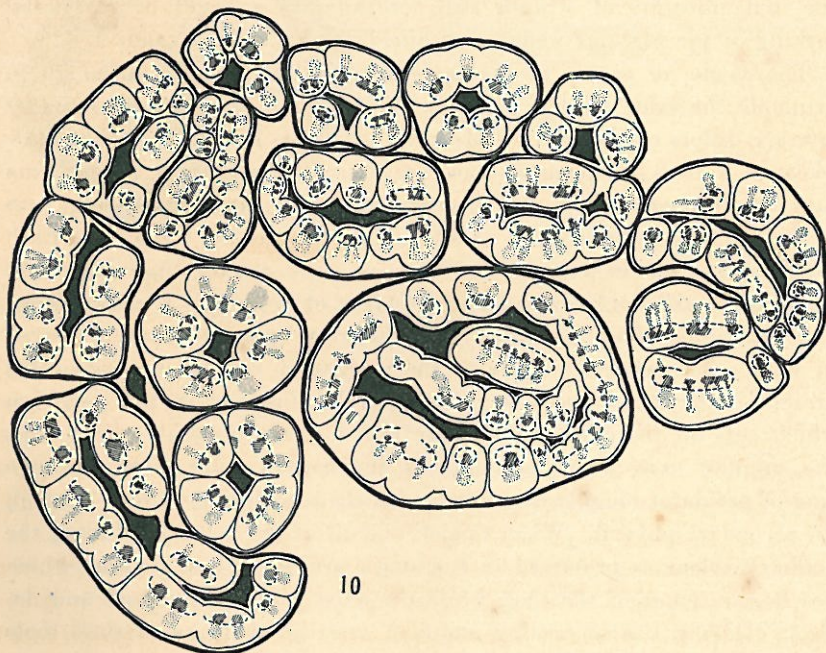


FIG. 10.—Cross-section of the tap-root shown in Pl. VIII, fig. 15, collected August 19 of the fourth summer of the plant's life (it is somewhat more than three years old). Vessels occur in the obliquely hatched areas, sieve tubes in stippled areas, cambium is indicated by broken lines, dead tissues by solid black. (Free hand,  $\times 2.5$ .)



root, may be cut out by a periderm, just as happens in the case of the tap-root, and has been described as "sporadic fission." The actual fission of the strands by this method has not been observed. In the spring following that in which the primary fission occurs, the newly formed portion of each vascular ray which the strand contains is isolated from the older tissue by periderm (Fig. 27). The cambium is produced through the intraxylary dilatation parenchyma, and the cycle of thickening, fission and thickening begins over again. Fig. 10 shows a tap-root of a plant in its fourth summer, which has accordingly gone through three periods of fission, and consists, at the level of the figure, of seventy-four separate strands, a number which would have been greatly increased in the following spring (Pl. VIII, fig. 15). As a plant becomes older, and consists of a greater number of strands, the intraxylary cambium in each does not as a rule initiate new vascular bundles before the next dissection in the following spring. The strand accordingly does not acquire a radial structure, and the new strands into which it becomes dissected lie all to one side, and are orientated in the same way. Nevertheless, the multiplication of strands still continues as a result of the radial forking of the vascular wedges contained in each older strand.

The course of events in the more slender lateral roots, although in principle the same as that just described for the tap-root and stronger laterals, differs considerably in detail. It will be remembered that these roots, as well as the primary root, are diarch. Two broad parenchyma rays are formed opposite the protoxylem points, and alternating with these are two sectors in which vessels and sieve-tubes are produced. Each sector may fork once or rarely more, or may remain undivided, and there are usually only two or three wedges of vessels in the thin roots. The thickening of the root may be symmetrical or more or less eccentric, in some cases extremely so, with the wedges of vessels and sieve-tubes directed entirely to one side. In the following spring the periderm which cuts off the older tissues may follow one of several courses. In the simplest case, which is found in the most slender roots, a single ring of periderm roughly concentric with the cambium is formed through the secondary phloem. When this occurs, all of the xylem, including the primary xylem, is preserved in the single strand of living tissue which lies in the center of the root, while the older phloem is cut off and decays. During the succeeding summer, one can distinguish such roots from the young roots, which have undergone no periderm formation inside the pericycle, only by the alternation of small and large vessels in the former, marking the transition from autumn to spring growth. In



other roots, and this is a method which is most likely to be followed in the more eccentric ones, the periderm encloses an open ring of tissue, for a deep embayment on the least thickened side of the root cuts out the central xylem. Usually the primary xylem is cut out by this invagination of the periderm (Fig. 11), but this is not always the case, for sometimes the embayment misses the primary xylem, while including a portion of the older secondary xylem to one side of it. Finally, in the case of extremely eccentric roots, the new strand lies entirely to one side of the center, and resembles that formed from a single sector in the hypocotyl. The same root which at its base is dissected according to one scheme, may follow another scheme nearer the apex, where it is more slender. One of the chief differences, then, between the weaker roots and the other perennating portions of the plant, tap-root and subterranean stems, is that in the former the central xylem sometimes sur-

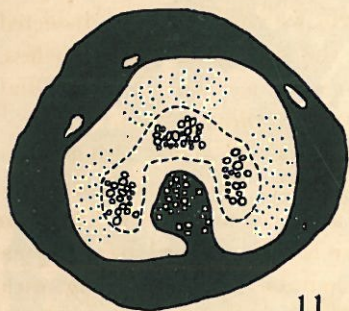


FIG. 11.—Cross-section of a slender root collected in the spring of its second year, showing the method of dissection. The symbols are the same as in Figs. 2-5. (Camera lucida,  $\times 17$ .)

11

vives the general pruning away of older tissues, which occurs every spring, and is included in the newly formed strand, while in the latter the primary xylem and the older portions of the secondary xylem are always cut away.

### ANATOMY AND FISSION OF THE STEM

Considerable study has been devoted to the anatomy of the etiolated shoot, and the important differences between this and the normal, green shoot are in general well known. It has been usual, however, in the investigation of the anatomical peculiarities which accompany etiolation, to grow the plants intended for study in darkness artificially produced, and the knowledge gained from these studies has been considered valuable chiefly in the interpretation of the physiological processes of the plant, much as the study of certain pathological conditions has thrown light on the normal physiology of the animal body. The knowledge of



the changes caused by etiolation are not usually essential, however, to the understanding of the structure of the plants of the same species growing in their natural habitat. In *Mertensia*, on the contrary, the peren-

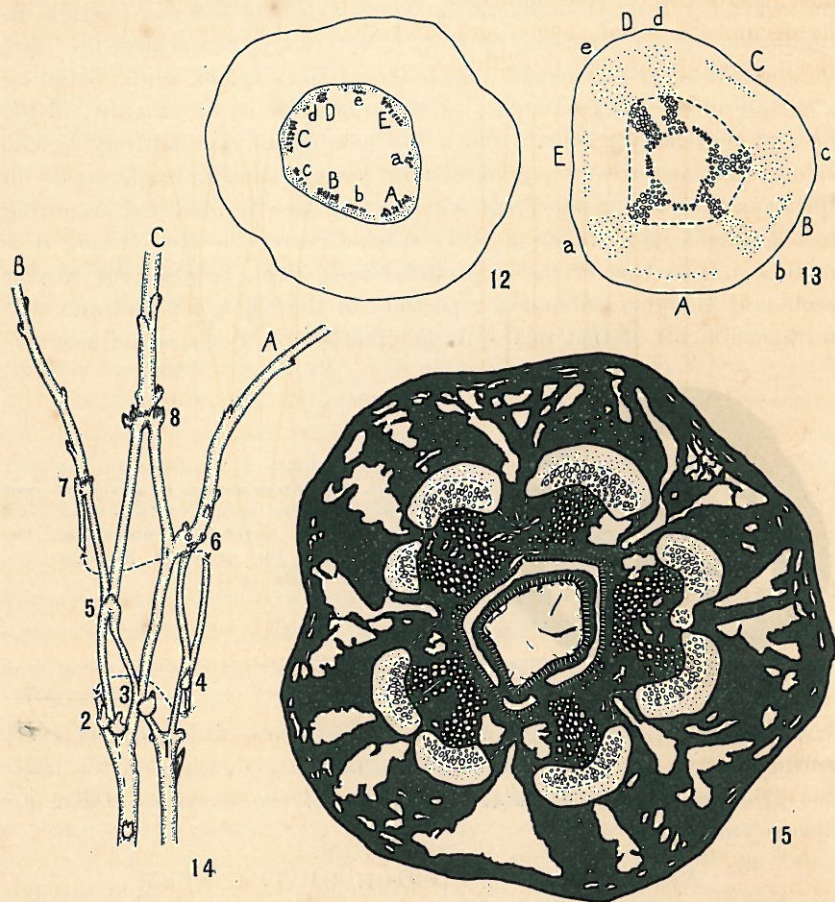


FIG. 12.—Cross-section of a young aerial shoot showing the arrangement of the common (A-E) and cauline (a-e) bundles, lettered to correspond with a section just below node 1 in Fig. 16. (Camera lucida,  $\times 8$ .)

FIG. 13.—Cross-section of the buried base of a stem about three months old, collected August 19. (Camera lucida,  $\times 9$ .)

FIG. 14.—The dissected base of a stem late in its second summer, showing the arrangement of the strands. The nodes are numbered 1-8. Three lateral branches of the dissected main axis are lettered A, B and C. For clearness, the strands have been cut in two places and spread apart. The severed ends are connected by broken lines ( $\times \frac{3}{4}$ ).

FIG. 15.—Cross-section of a very vigorous 1-year-old buried stem, collected in early June, showing its dissection at this level into eight strands. The symbols are those used in Figs. 3-5. (Camera lucida,  $\times 8$ .)



nating etiolated bases of the shoots play an important rôle in the economy of those plants which have been buried by the shingle, and their anatomy, differing fundamentally from that of the shoots growing in the light, must receive careful consideration. We shall treat first the structure of the decumbent aerial shoots, and later that of the bases of the shoots which grow up through the shingle.

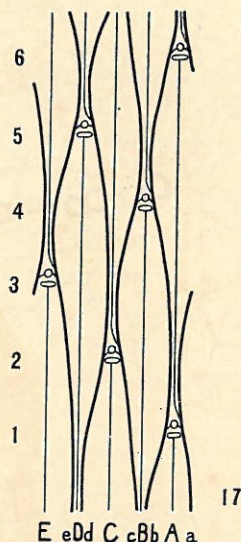
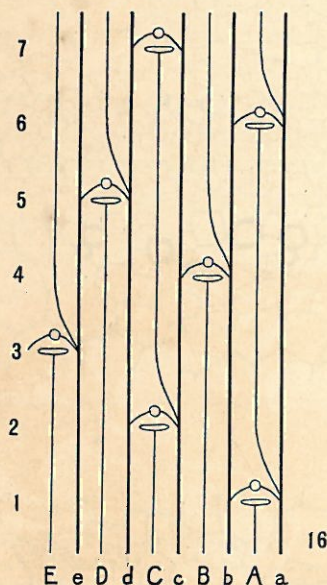


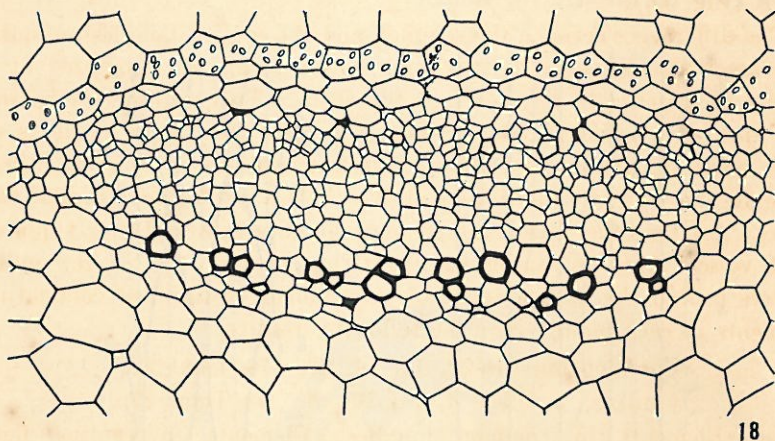
FIG. 16.—Diagram to show the course of the vascular bundles in an aerial or very vigorous buried stem. The common bundles (A-E) are indicated by thin lines, the cauline bundles (a-e) by heavy lines.

FIG. 17.—Diagram to show the course of the bundles in a more slender buried stem.

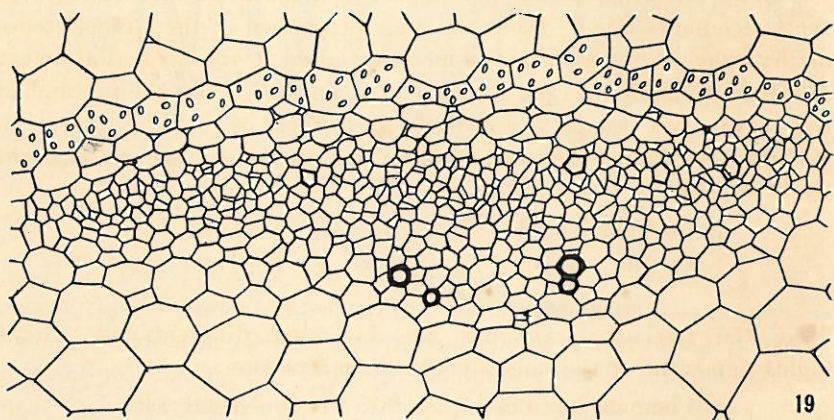
The phyllotaxy of *Mertensia* is  $\frac{2}{5}$ , and the spiral on which the leaves lie may be either right-handed or left-handed. A cross-section through a young, unthickened, aerial shoot reveals usually ten broad, shallow vascular bundles (Figs. 18 and 19) five of which contain considerably more protoxylem elements than the other five which alternate with them (Fig. 12). The five stronger bundles are common bundles or leaf-traces, the alternating weaker bundles are cauline. The cauline bundles (Fig. 16 a-e) run straight up the stem. Whenever a cauline bundle passes the proximal side (as one follows the spiral of phyllotaxy up the stem) of a leaf insertion, it gives off a branch on its own distal side. This branch becomes the common bundle which replaces the one that



has just bent out into the petiole, runs straight up the stem through five internodes and enters the next leaf above in the same orthostichy. Thus all of the leaves of the same orthostichy are entirely dependent upon the same cauline bundle. In the base of the petiole the common bundle gives off branches to the right and left, which in turn imme-



18



19

FIG. 18.—A common bundle in an internode 6 mm. behind the apex of a shoot collected in early June. The cambium is just beginning to differentiate. The starch-sheath may be followed by its included starch grains. Notice the lacunæ left by the disruption of the earliest protoxylem and protophloem elements, some of which are already clogged by a darkly staining substance ( $\times 235$ ). This is not the bundle which leaves the stem at the next node above.

FIG. 19.—A cauline bundle at the same level ( $\times 235$ ).

(Both figures from camera lucida sketches.)



diately branch several times to form the subordinate bundles of the petiole. So the broad, channeled petiole comes to have a strong central bundle and from three to seven weaker bundles of various degrees of development on either side of it. The branch traces, two in number, arise from the two cauline bundles which pass on either side of the leaf-trace (Fig. 16).

The differences between the common and the cauline bundles are quite fundamental, and with a little practice each can be recognized at a glance at practically any level of the shoot. Two millimeters behind the apex of a rapidly growing shoot the first protoxylem elements of both types of bundles have become lignified, so there is no great difference in the time of maturation of the earliest protoxylem in the two types. On the other hand, the common bundles are far better supplied with vessels than the cauline bundles (Figs. 18 and 19). A few millimeters behind the apex a count of the number of lignified conducting elements in each bundle gave the following results:

Common bundles—22, 12, 14, 23, 11—Total 82.

Cauline bundles—4, 4, 10, 4, 5—Total 27.

Ratio—Elements in common bundles: Elements in cauline bundles :: 3:1.

Despite this difference in the number of differentiated elements, both types of bundles occupy about the same proportion of the circumference of the stele. Although there is much variation in the tangential extent of different bundles of even the same type, on the average the procambial cells of one type occupy arcs about equal to those of the other type. In the third elongated internode behind the condensed apex, the count stood as follows:

Common bundles—32, 22, 14, 32, 19—Total 119.

Cauline bundles—15, 12, 6, 9, 8—Total 50.

Ratio—2.4:1.

Here the fascicular cambium was becoming differentiated. In the eighth internode of the same stem the numbers were:

Common bundles—44, 25, 37, 24, 30—Total 160.

Cauline bundles—15, 21, 12, 19, 27—Total 94.

Ratio—1.7:1.

At this level the interfascicular cambium was becoming differentiated. Already the most recently formed tracheæ in the cauline bundles were of considerably greater diameter than those in the common bundles. In the twelfth internode:



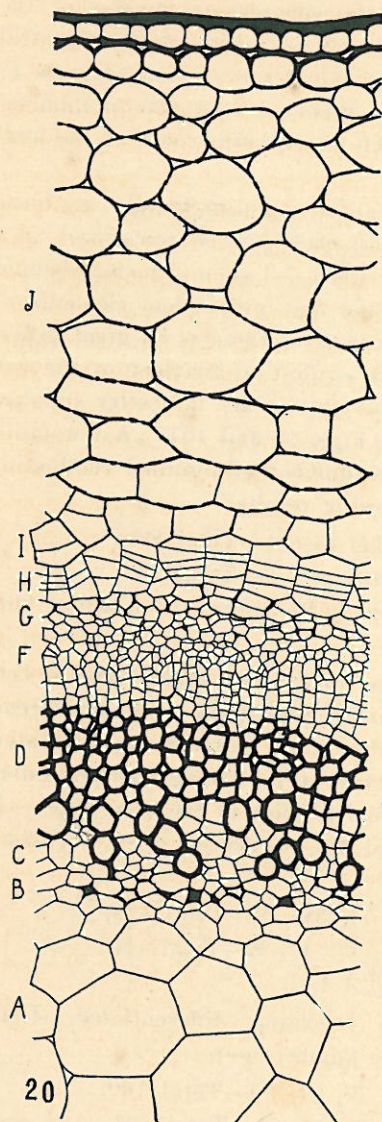


FIG. 20.—A strip through a secondarily thickened common bundle about 18 cm. from the base of an aerial stem collected on August 19 of its first summer ( $\times 150$ ).

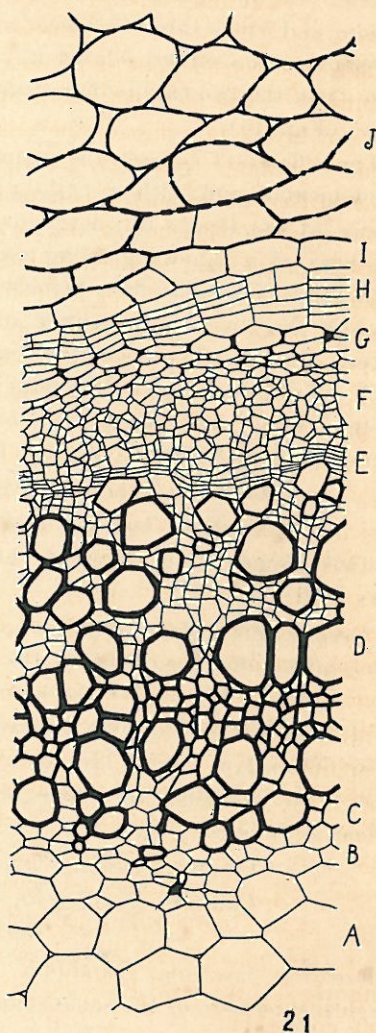


FIG. 21.—A strip through a nearby cauline bundle ( $\times 150$ ).

From bottom to top of both figures: A = pith, B = protoxylem, C = metaxylem, D = secondary xylem, E = cambium, F = secondary phloem, G = primary phloem, H = periderm, I = endodermis, J = cortex. (Both figures from camera lucida sketches.)



Common bundles-62, 44, 53, 28, 52—Total 239.

Cauline bundles-36, 41, 22, 28, 46—Total 173.

Ratio—1.4:1.

At this level considerable secondary xylem had been formed in both sets of bundles. The mere statement of the number of conducting elements does not give a fair idea of the relative importance of the two types of bundles in water transport, for the average diameter of the vessels in the cauline bundles was considerably greater than in the common, and so the relative efficiency of the former was very much greater than appears from the bald numerical statement. From this time on an active cambium continues to augment the number of vessels in the cauline bundles, while few or none are added to the common bundles, so that by August the difference in the appearance of the two types is very striking (Figs. 20 and 21). The lumina of the largest vessels present in the cauline bundles at this time average  $58\mu$  in diameter, while those of the common bundles average only  $32\mu$ . The average cross-sectional area of the former is more than three times as great as that of the latter, and their efficiency in conduction correspondingly greater.

This inversion of the relative development of the two types of bundles as growth proceeds is exactly what one would expect on the assumption that the degree of development of the conducting elements is conditioned by the demands made upon them by transpiration. In the fifth internode behind the youngest actively transpiring leaf no cauline bundle is needed for conduction, except to supply the relatively slight water requirements of the growing point, while each of the five common bundles must take care of the transpiration stream directed to a transpiring leaf (Fig. 16). In the eleventh internode each of the cauline bundles must take care of one transpiring leaf, and one of them of two; in the sixteenth, all with two and one with three, etc., while no common bundle ever supplies more than one leaf. Since the aerial stems of *Mertensia* as a rule remain unbranched, the water supply of the dormant or only slightly active lateral buds has been left out of consideration in the present discussion.

After the initiation of the cambium a complete ring of lignified secondary xylem is laid down, a condition found in a number of other herbaceous Boraginaceæ. This ring consists of tracheæ of the sort already familiar to us in the root, lignified parenchyma cells, transitional forms between these and fibres, and relatively few genuine fibres of the libriform (simple-pitted) type. In Fig. 22, e is a parenchyma cell, similar in shape to those which make up the bulk of the secondary xylem



of the root and subterranean stem, and of the same length as the cambium cell from which it was cut off, but with its walls thickened, lignified and penetrated by simple pits. These cells lie in horizontal, radial series, as has already been described for the root. In the same figure, **b, c, d, f, g, h** and **i** are cells of this general shape which have sent out one or more processes, in shape often reminiscent of the pseudopodia of a rhizopod, which have advanced by sliding growth between the ends of the cells of the next series above or below, while the bodies of the cells maintain regular horizontal ranks. In cross-sections (Figs. 20 and 21) the smaller lumina lying between the corners of the large cells making up the schlerenchyma ring are those of the processes from the cells of the next series above or below the level of the section. True fibres, such as that represented in Fig. 22, **a**, are much rarer than these transitional forms.

In the common bundles, the cambium gives rise to four or five layers of schlerenchyma cells in which few or no vessels are included, then to a few layers of unligified parenchyma cells and by the middle of August has become inactive (Fig. 20). There is some variation in the degree of development of different bundles, or rather of different levels of the same bundle. Near the insertion of the leaf which it supplies, the formation of vessels in the secondary xylem of the common bundle is rare, while at the other end of the bundle, near its point of origin from the cauline bundle, a few vessels may be scattered in the schlerenchyma, and an occasional one may be formed after the schlerenchyma ring has been completed. Where a common bundle lies close between two cauline bundles—a condition which often occurs near its point of origin from one of them—it may be thickened much as is the latter. In the cauline bundles many large vessels interrupt the schlerenchyma ring, and after forming five or six layers of schlerenchyma cells, the cambium continues to form numbers of large vessels separated by thin-walled parenchyma cells. In late August, at a time when the cambium of the common bundles has become entirely quiescent, that in the cauline bundles is in a state of active division (Fig. 21). The interfascicular cambium never gives rise to any conducting elements, so the vascular bundles remain entirely distinct. After forming a few layers of cells which complete the schlerenchyma ring, this portion of the cambium gives rise to thin-walled parenchyma alone. Near the apex of the shoot the lignified cells are thin-walled or locally absent, and a continuous ring of schlerenchyma is not formed. Here, too, since the degree of secondary thicken-



ing is much less, the contrast between the two types of bundles does not become so pronounced as nearer the base of the shoot.

The pericycle and phloem consist of thin-walled cells, and pericyclic or bast fibres, which are usually absent in the Boraginaceæ (*Heliotropium*, with pericyclic fibres, constitutes an exception) are not formed in *Mertensia*. The sieve-tubes of the protophloem are early disrupted, and their cavities, more or less occluded by the neighboring parenchyma cells, become filled with a dark-staining substance (Figs. 20 and 21). As with the xylem, so there is a markedly greater development of the secondary phloem in the cauline than in the common bundles, where at most one or two layers which include sieve-tubes are formed.

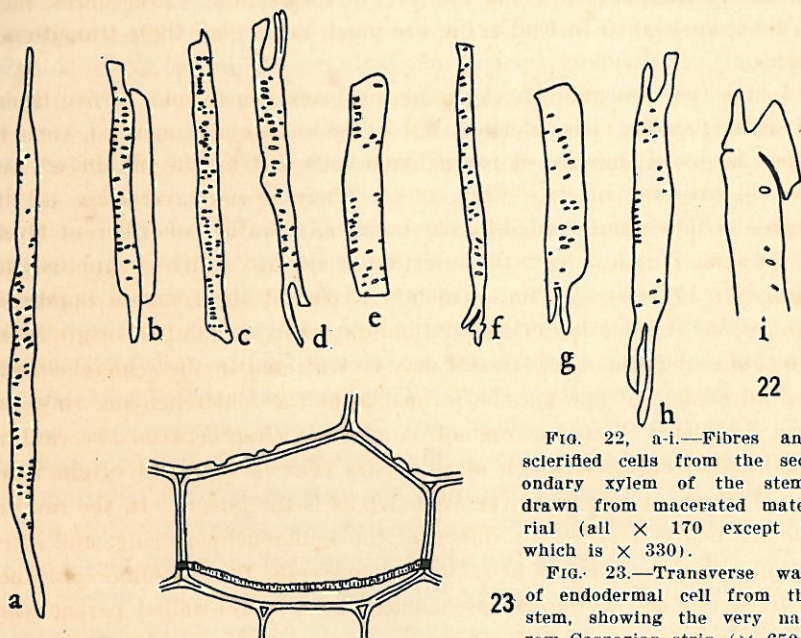


FIG. 22, a-i.—Fibres and sclerified cells from the secondary xylem of the stem, drawn from macerated material (all  $\times 170$  except i, which is  $\times 330$ ).

FIG. 23.—Transverse wall of endodermal cell from the stem, showing the very narrow Casparian strip ( $\times 650$ ).

In the lower half of the stem a distinct endodermis is present, its cells characterized by a very narrow Casparian strip, which is situated near the inner tangential wall (Fig. 23). In the upper portion of the shoot a starch-sheath takes its place. I have found no mention of an endodermis in the stem of the Boraginaceæ, and Jodin does not describe or figure it. In *Mertensia virginica*, which I examined, an endodermis of the type present in *M. maritima* surrounds the stele in all but the most apical portions of the stem, and an arc of it subtends the abaxial side



of each of the vascular bundles through the petiole. At the base of the shoot of *M. maritima* periderm may arise tardily in the pericycle, and in one stem as many as eight layers of cells had been formed by August, but even here the primary cortex persists throughout the life of the aerial shoot. The cells of the inner region of the cortex (Fig. 20) are large, with walls prominently but rather unevenly thickened, and penetrated by conspicuous pits. They merge gradually into an outer region of smaller cells which in places are rather irregularly collenchymatous, and are separated by large intercellular spaces. The pith is composed of large cells, which in thick, vigorous shoots break down and leave a medullary cavity. It is not, however, cut out by a periderm, as in the case of the etiolated shoot.

We have next to consider the etiolated shoots, which in the spring push out from the dormant buds of plants recently buried by the shingle, and make their way up through the overlying stones. In forcing their irregular passage, these slender, brittle, white shoots, bearing leaves reduced to scales, become extremely contorted, so that it was found impossible satisfactorily to determine their phyllotaxy by external count. To add to the confusion, a cross-section of the more slender of them reveals six, five or, more rarely, only four vascular bundles in the narrow stele. Fortunately the more vigorous of these shoots show the normal ten bundles, and by following down a series arranged in the order of increasing reduction it is possible to account for the vascular structure of even the most slender of them. The course of the bundles was plotted from camera lucida drawings made from serial hand-sections, and it was found that the diagrams could be systematized only on the assumption that the phyllotaxy remained the normal  $\frac{2}{5}$ , even although the number of bundles found in a cross-section was reduced to six or five.

The type of stele most frequently encountered in buried shoots shows six or sometimes seven bundles in cross-sections made at various levels of the same stem. Pl. IX, fig. 18, shows such a stem after it has been secondarily thickened. Such a condition arises in the following manner: To begin with we must recognize ten bundles, five common and five cauline (Fig. 17), although in any cross-section several of these are so closely associated that the medullary ray does not develop between adjacent bundles, and they are accordingly indistinguishable. Thus, when the leaf-trace **A** bends into the petiole at node 1, the cauline bundles **a** and **b** become confluent above the leaf gap. The common bundle **A**<sup>1</sup>,\*

\* In like manner bundle **B**<sup>1</sup> replaces **B**, **C**<sup>1</sup> replaces **C**, etc., after the latter have bent out to supply their respective leaves. All bundles bearing the same capital letter lie in the same vertical rank, and are not designated separately in Figs. 16 and 17.



which replaces **A** and which in a vigorous green shoot would separate from **a** near this level, remains sandwiched between the two. In the internode between nodes 1 and 2 we have a single bundle **bA<sup>1</sup>a** with a triple valence. First, about one internode higher up, the cauline bundle **a** branches off to the right to join **e** above the insertion of the leaf at node 3, then, somewhat higher up, **b** separates to join **c** above node 4, leaving **A<sup>1</sup>** to continue alone to its leaf at node 6. In any internode, we usually find three distinct common bundles, which will enter the first three leaves above, one distinct cauline bundle, and two common bundles each surrounded by two cauline bundles. The composite bundle generally occupies a greater arc than any single bundle, and after it has become secondarily thickened, it can generally be distinguished by the fact that the vessels lie in two arms. In Pl. IX, fig. 18, the large cauline bundle at the top of the figure is single, the broad bundles at the right and left are, as explained, triple. These alternate with three inconspicuous common bundles. A much slighter degree of fusion between bundles (i. e. between **bBc** and **dDe**) is evident in Fig. 13. The smaller metaxylem elements of the common portion of a triple bundle can frequently be picked out in the midst of the larger vessels belonging properly to its cauline components.

In still more slender etiolated shoots, a reduction to only four distinct bundles has been observed. The whole group **cBb** (Fig. 17) may fuse with **a** above node 1, instead of **b** alone separating from **cB** and forming the fusion. Thus we obtain the following grouping of bundles:

(E) (eDd) (C) (cBbA<sup>1</sup>a)

Somewhat higher in the internode the bundles separated as follows:

(E) (eDd) (C) (cB) (bA<sup>1</sup>a)

In the formation of an independent common bundle, say **D**, **Dd** first separates from **e**, and then **D** separates from **d**. Such a drastic reduction in the number of bundles as that illustrated above is rare but, as a rule, the weaker the shoot, the longer such groupings as (**bBa**) and (**cBb**) remain confluent.

As in the green aerial shoot, the common bundles in the etiolated shoot, at first better developed than the cauline bundles, lag behind them in secondary thickening. Indeed, the difference in the production of conducting elements is here still more pronounced, because these common bundles never supply any transpiring leaves, while the cauline bundles must take care of all of the leaves which the shoot develops after it emerges from the shingle. The schlerenchyma ring is completely suppressed in the buried stem, and the elements of the secondary xylem and phloem are identical with those of the root. The cauline bundles are



thickened by the addition of vessels separated by parenchyma cells on the one side, and by sieve-tubes separated by parenchyma on the other. In the common bundles a few conducting elements are sometimes added during the early part of the season, but thereafter parenchyma cells alone are formed, and the group of sieve-tubes in the primary phloem becomes separated from the group of vessels in the primary xylem by a broad expanse of uninterrupted parenchyma. By late August the cambium of the common bundles, which has never produced as many layers of cells as that of the cauline bundles, becomes inactive and occasionally disappears entirely from the center of the bundle. In this respect the common bundles resemble the parenchyma rays of the root. Although no conspicuous embayment of the cambium is observable here, the thickness of secondary xylem and phloem on the radii of the common bundles is considerably less than that on the radii of the cauline bundles, with the result that the stem as a whole, as well as the cambium ring, becomes angular, with the cauline bundles lying at the angles (Fig. 13). As in the root, the distribution of oil globules follows that of the active conducting elements. While globules are not rare in the secondary xylem parenchyma of the common bundles, they are scarce in the secondary phloem, where they would lie in cells still farther removed from the active conducting elements of the cauline bundles. An exception to the general behavior described for the common bundles in this paragraph is found where these are so closely associated with cauline bundles on either side of them that the thickening of the three fused bundles proceeds almost as a unit.

The starch sheath present at the apex of the etiolated shoot becomes altered a few millimeters farther back into a typical endodermis with Casparian strips usually broader and more prominent than those described for the aerial stem, upon which the starch disappears from these cells. Casparian strips could never be traced beyond a point that was still 15-20 cm. from the apex of a rapidly growing green shoot. Priestley (17) found that in the etiolated shoots of *Vicia* and *Pisum* the starch sheath rapidly became converted into a true endodermis, although in the normal stem of these species it is present only at the very base, and that with the formation of the Casparian strip the starch disappeared from the cells. In the etiolated shoots of *Mertensia* a phellogen arises beneath the endodermis in the outermost layer of the pericycle, just as it does in the root, and the primary cortex dies away, so that by the middle of August no trace of it remains. As in the hypocotyl, the initia-



tion of this phellogen is preceded by the suberization of the entire wall of the endodermal cells. The cauline periderm resembles that of the root in its degree of development.

The pith also is always cut off from the living tissue by a periderm, just as in the root the central portion of the xylem is sometimes cut out (Pl. IX, fig. 18). The pith in the slender etiolated stems is usually solid, not hollow as in the thicker aerial stems. At about the same time that the phellogen arises in the pericycle, the walls of the outermost layer of the large cells of the central pith become suberized. The smaller cells of the layer external to this then divide by tangential walls, and a phellogen which completely surrounds the pith is organized. The medullary periderm usually consists of a few more layers of cells than the external periderm.

From what has been said it can be seen that the buried shoot, in its secondary development, very closely resembles the hypocotyl and root in the following particulars:

1. There is an endodermis beneath which arises a periderm cutting off the primary cortex. The development of this periderm is very similar in both organs.

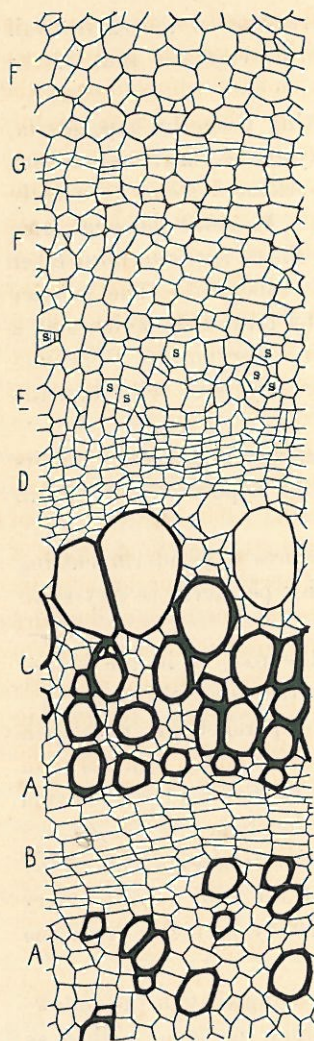
2. Schlërenchyma is not formed either in the root or in the buried stem, and the secondary xylem and phloem are the same in both.

3. Just as the cambium is less active in the parenchyma rays than in the vascular segments, so it is less active in the common bundles than in the cauline. It often dies out in August both in the broad parenchyma rays of the root and in the common bundles of the stem.

4. The central portion of the stem (the pith) is always cut off by periderm, and similarly the central portion of the root (the primary and some secondary xylem) is sometimes cut off by periderm from the more active tissues.

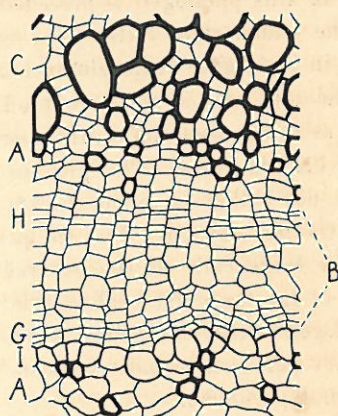
Considering these resemblances, it is not surprising that in the following spring the dissection of the stem should follow the same method as that of the root. In the material collected in early June the cambium of the cauline bundles had become very active, and had formed numbers of large vessels which contrasted sharply with the small vessels formed in the previous autumn (Fig. 15). The local thickening had resulted in the deep embayment of the cambium ring over the common bundles. This portion of the cambium was totally inactive, perhaps already dead. The strains set up by the unequal growth in thickness resulted in numerous rents in the parenchyma of all regions, the most conspicuous of





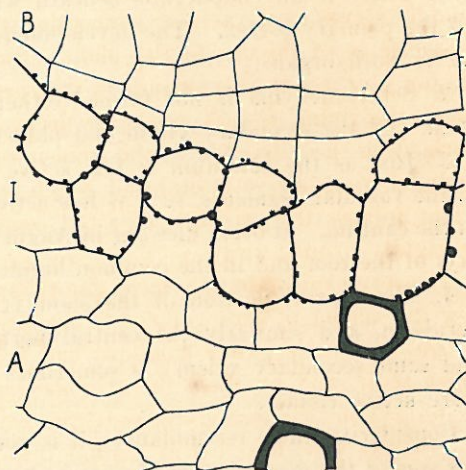
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FIG. 24.—A radial strip through one of the strands of the stem depicted in Fig. 15, showing, from bottom to top, the narrow vessels formed at the end of the previous growing season (A), the dilatation parenchyma which arises between these (B), the large spring vessels (C), the very active cambium (D), the newly formed phloem (E) and the old phloem (F) interrupted by the outer phellogen (G). ( $\times 140$ .)



25

FIG. 25.—Detail from the tap-root in Fig. 4, showing the formation of cambium (H) and phellogen (G) in the dilatation parenchyma (B). ( $\times 140$ .)



26

FIG. 26.—Detail from the cross-section of a tap-root treated with alkannin, showing the layer of suberized cells (I) which surrounds each strand before the periderm is differentiated, and the numerous oil globules which lie against the walls of these cells ( $\times 535$ ).  
(All figures from camera lucida sketches.)



which were large, triangular lacunæ which developed on the radius of each common bundle. The histology of the formation of a phellogen around the new tissue of each cauline bundle, and the completion of the cambium ring surrounding the xylem of each new strand by its production through the intraxylary dilatation parenchyma are so similar to what occurs in the root that to describe it would be needless repetition. It is only necessary to add that a new medullary periderm arises beneath the old one and cuts off the latter, which now lies free in the central cavity of the shoot, and may be pulled out in the form of a long, corky tube. This last burst of meristematic activity on the part of the outermost perimedullary cells seems utterly useless, for in a short time they, together with all of the tissues which surround them, will cease to be a portion of the living plant.

The course and development of the strands into which the stem disintegrates is determined by the arrangement and activity of the lateral buds. In the previous autumn the terminal aerial portion of each shoot had died and during the winter it had decayed, so that now unless a bundle serves as a vascular connection for a lateral bud or branch, its presence is of no use to the plant. Such useless portions of bundles do not give rise to new strands in the spring, but are cut off by periderm from the living tissues and soon decay away. Every strand which is formed on the dissection of the stem is in actual service as a conducting channel to an active lateral bud which is developing into a shoot. The plant follows the principle of strict economy and every useless portion is rigidly pruned away.

If every cauline bundle gave rise to a single strand, these would follow the scheme of arrangement of the heavy lines in Fig. 16. Wherever a cauline bundle passes a lateral bud or branch, it gives off a branch-trace to it, and by these the strands are joined in pairs at successive nodes. Thus the strand derived from cauline bundle *c* would be joined alternately with *b* and *d* at regular intervals, *d* with *c* and *e*, etc. In passing to the left, from *c* to *e*, the strand *d* runs free through three internodes, in passing to the right, from *e* to *c*, the same strand runs free through two internodes. Such a regular arrangement of strands is sometimes found, and Fig. 14 illustrates an actual case of this.\* Here we have, formed entirely by the activity of the plant, a solid model illustrating the course of the cauline bundles. Unfortunately, one may

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\* It should be noticed that while Figs. 16 and 17 are based on a left-handed spiral of phyllotaxy, Fig. 14 is drawn from a shoot with a right-handed spiral. The text refers to the former figures.



often examine dozens of dissected stems in a vain search for such perfect examples, for they are quite in the minority. The reasons for the failure of most stems to show the expected pattern are several:—

1. Unless a lateral bud actually becomes active in the spring, the bundles upon which it is immediately dependent do not form new strands, but decay during the ensuing summer. It will be noticed that above node 7 in Fig. 14 there are only two strands, those which supply the branch C arising from the next node. A large plant, which had not been deeply buried in the second winter previous to our examination of it, may have sent up a great many stems, the short buried portion of none of which bore three buds active in the spring during which its dissection occurred. It will be seen that unless there are at least three branches, not enough strands to fill the pattern will be preserved. One finds many flowering shoots apparently bifurcated at the base. These two strands represent all that is left of the parent stem of which this is the only branch.

2. Because of the fusion of bundles so frequent in the more slender stems, the newly formed portions of two fused cauline bundles are incorporated in the same strand, with the result that only a single strand is found immediately above a bud. This strand soon forks, however, as its two components must supply different buds higher up, and even where it is externally single, a cross-section usually reveals its double valence. It may contain two cambium rings, or a single one with a bifurcated bundle.

3. A single cauline bundle may be divided into more than one strand. When a vigorous, young plant has been deeply buried, it usually sends up one or two shoots into which all of its energy of growth is thrown (Pl. VII, fig. 14). These shoots, unlike most of the etiolated shoots, not only show the full number of distinct bundles in cross-section, but some of the cauline bundles may fork, and in the following spring each fork gives rise to a strand, just as occurs with each wedge of vessels and sieve-tubes in the root. The stem shown in Fig. 15 has given rise, in this manner, to eight distinct strands at the level of the cross-section. In another stem as many as fourteen strands were counted at one level. Strands representing the same cauline bundle can be recognized by the circumstance that they usually anastomose among themselves between their connections at the buds with other cauline bundles, but there is never any anastomosis between strands from distinct cauline bundles.

The subsequent history of the strands into which the stem falls as the dead tissues in which they are imbedded decay away, presents no new points of interest. One would be at a loss to distinguish, from its appearance in cross-section alone, a strand arising from the dissection of the stem from one arising from the dissection of the root. Each stem strand becomes dissected anew every spring precisely as in the root. All of the strands representing the dissection of a single cauline bundle usually remain connected at the nodes where the bundle gave off branch traces to a lateral bud. At some of the nodes there develops a great swollen mass containing dozens, possibly hundreds, of dormant buds (Pl. V, figs. 10 and 11). This is apparently by the slow growth and multiplication of the buds axillary to the scale leaves of the originally single axillary bud. A similar mass of buds originates at the crown of the hypocotyl from the buds axillary to the leaves of the rosette (Pl. VII, fig. 13; Pl. VIII, fig. 15). These buds constitute an organ reserve which may be called into service in the event of an accident to the more terminal portions of the plant.

If one tugs gently at any bundle of strands derived from the stem of an old, dissected plant, such as that shown in Pl. VIII, fig. 16, he will usually find that a certain number of divisions of the tap-root, bearing in turn lateral roots, will readily tear away from the mass of the plant along with it. Such a detached portion is in one sense a complete individual, with roots, stem and leaves and, if it were planted carefully, there is no apparent reason why it should not continue to thrive. Thus there is always a most intimate connection between certain absorbing, conducting and transpiring elements, and this is preserved through every subsequent dissection of the plant. Since this is the case, it becomes easier to understand why, when a leaf withers, the downward prolongation of its vascular bundles should be of no further service to the plant, and so should be removed from it. In *Mertensia* we have a beautiful argument in favor of the now discarded botanical philosophy that the whole stem and root of the plant are merely an aggregation of basally prolonged leaf traces!

#### ORIGIN AND SIGNIFICANCE OF THE HABIT OF FISSION

Apparently there is no mention in the literature either of the aberrant behavior of *Mertensia maritima* described in the present paper, or of any abnormality in the secondary thickening of the axis of any other



member of the genus. It is rather surprising that the remarkable structure of a plant so widespread and of such striking appearance as the sea lungwort should remain so little known. No mention of the occurrence of abnormal secondary thickening of the axis of any of the more than 1500 species of the Boraginaceæ is found in either the comprehensive works of Schenck (20), Solereder (22) or Pfeiffer (16), or in any of the shorter papers which have been consulted. The single partial exception to this statement lies in the species *Tournefortia hirsutissima* L., a tropical climber with a woody axis penetrated by narrow plates of secondary phloem, as first described by Crüger (3), who does not state whether the cambium is continuous along the sides of the indentations or not. At any rate, we do not have here any inverted secondary bundles, or any complexities of growth at all comparable with those found in lianas of other families and in *Mertensia maritima* in the same family. The very fact that the sea lungwort should have remained so long anatomically unknown, however, makes one extremely cautious about affirming anything definite concerning the family as a whole, with its large number of tropical representatives.

It is of interest to compare the anatomy of the sea lungwort with that of its congener, the Virginia cowslip [*M. virginica* (L.) Link.]. It is hard to imagine two plants of the same genus with more varied habitats, for while the former thrives on stony, exposed seacoasts, the latter prefers sheltered, wooded valleys of the interior, where it grows in deep, rich, alluvial loam. The erect stems arise from tap-roots, which, while young, are usually spindle-shaped and often forked, but in age may become very irregular (Pl. IX, fig. 17). These tap-roots, like those of *M. maritima*, contain no fibres in wood or bast, but merely the vascular elements imbedded in succulent parenchyma. The outer secondary cortex is cut off by a periderm every spring, and in older, larger tap-roots the central xylem is also cut out by periderm, but there is considerable irregularity in this respect. This tissue then decays and leaves a central cavity. The largest tap-root examined by me measured 4 cm. in diameter at its widest part, and contained a central cavity 2.5 cm. in width. Once the central cavity is formed, a new ring of periderm cuts off the oldest surviving xylem at the renewal of growth every spring, at the same time a concentric ring of periderm cuts off the older phloem on the outside. Rarely the periderm may penetrate along the primary parenchyma rays and after the tissue which it cuts off has decayed away, the interior cavity communicates with the exterior.

Fig. 28 shows a cross section of the tap-root which of all those examined bore the greatest resemblance to *M. maritima*. It was split into two distinct portions for a short length only. The plant was collected in the spring, and the xylem and phloem most recently cut off were still fresh. The tissues cut off in the previous spring, now decayed beyond recognition, surround the root and fill the central cavity, and

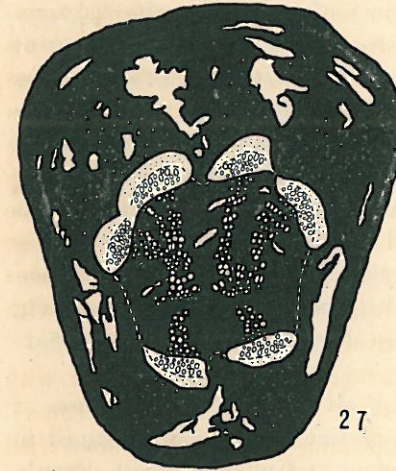


FIG. 27.—Cross-section of a primary division of a vigorous stem, collected in early June, at the beginning of its third growing season, showing its secondary fission at this level into five strands. Symbols as in Figs. 2-5. (Camera lucida,  $\times 10$ .)

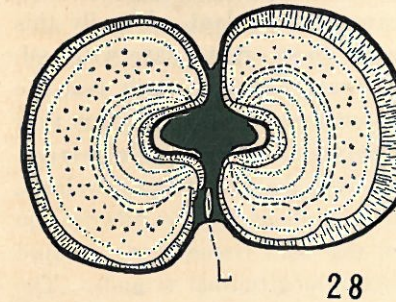


FIG. 28.—Cross-section of that root of *Mertensia virginica* which most resembled *M. maritima* in its mode of splitting. From material collected in Baltimore County, Maryland, on May 22nd. Older, dead tissue is shown in black, tissue just cut off by periderm is indicated by radial lines, cambium by broken line, L=lateral root ( $\times 2$ ).

in the figure are shown in solid black. It will be seen that in neither half has the cambium closed about the interior of the xylem to form a complete ring. The root in question bears more resemblance to a root of *M. maritima* which has undergone "sporadic" fission than to one which has passed through the winter and undergone "universal" fission in its second spring. In the cutting off of older tissues, however, we find an adumbration of the habit which is carried to its ultimate expression in *M. maritima*.



Until the time of fission, there is nothing unusual about the anatomy of the axis of *M. maritima*. It closely resembles that of *M. virginica*, surprisingly so considering the diverse habitats of the two plants and, as we have already seen, agrees closely in its general plan of structure with the herbaceous European Boraginaceæ as we know them through the work of Jodin (10).

The classic work on the split rhizomes of perennial herbaceous plants is that of Jost (11), and a brief summary of the whole subject, carrying the literature concerning it down to date, is found in the recent monograph of Pfeiffer (16). Splitting of the rhizome regularly occurs in *Gentiana cruciata* and allied species, *Corydalis nobilis*, *C. ochroleuca* and other Fumariaceæ, *Aconitum Lycoctonum*, *Delphinium elatum* and *D. scaposum*, *Salvia pratensis*, *S. silvestris* and *S. austriaca* and *Sedum aizoon*. In America the subject has not received so much attention as in Europe, and *D. scaposum*, described by Kingsley (13), is the only American species included in the list above. Of interest in this connection is the method of vegetative multiplication through the splitting of the root and basal portion of the stem described by Dastur and Saxton (4) for *Crotalaria buhria*.

The essential feature of the behavior of all hitherto described cases of split rhizomes is the isolation from the portion of the plant destined to remain alive of all vascular tissues—xylem and phloem—most directly connected with the annual stem and leaves of the plant. Usually this first occurs in the plant's second year, after these organs have withered. The process is repeated year after year, always with the result that the oldest remaining xylem and phloem are removed, since the organs they served are no longer in existence. In *Gentiana*, *Aconitum*, *Delphinium* and *Salvia* the useless portions are cut off from the living by a periderm, while in *Corydalis* the separation is brought about by the suberization of the walls of preexisting cells. When the dead tissues have decayed away, the living portions remain as distinct longitudinal strands. The first dissection of the rhizome is a result of the isolation of the cauline bundles (the fusion bundles of Jost), which are held together by the vascular connections of the lateral buds. In *Gentiana cruciata* the opposite, decussate leaves are supplied by four cauline bundles alternating with the four ranks of leaves, and in the dissection of the rhizome these remain as four distinct pillars, pairs of which are straddled by the two traces of each of the lateral buds, as was described long ago by Irmisch (9). The leaf-insertions are very close together, and the presence of the lateral bud often crowds to one side the insertion of the

leaf next above, a circumstance which gives a spiral twist to the orthostichies and leads to a complication of the form of dissection. In both *Corydalis* and *Aconitum* the common bundles (leaf traces) are cut away from the tissues which remain alive, and only the cauline bundles become a permanent portion of the plant—a condition we find exactly paralleled in *Mertensia*. Through the forking of the rays of vessels, and the disintegration of the parenchyma rays which arise between them, the strands representing the cauline bundles are further subdivided.

The roots of *Aconitum*, *Delphinium*, *Corydalis*, *Gentiana* and *Salvia* are split as well as the rhizomes. In *Gentiana cruciata* the vessels of the secondary xylem lie in rays which alternate with rays consisting of parenchyma alone, much as has been described for *Mertensia*. The cambium across the parenchyma rays becomes inactive, also as in *Mertensia*. Along these rays the periderm which isolates the central portion of the xylem becomes confluent with the periderm which cuts off the older phloem, and in this manner the root becomes split into distinct strands. In the diarch roots of *Corydalis* broad parenchyma rays continue the radii of the protoxylem points. The cambium across these rays dies out, and the starch disappears from these cambium cells, from the rays themselves, and from the outer phloem and the inner xylem. The cells of these rays and the older xylem and phloem lose their protoplasmic contents and their walls take on a brown color. During the course of the summer they decay away, leaving the root divided into two portions, which are bound together by the lateral roots, or by their separate strands after these in turn have become divided, as we have described for *Mertensia*. In succeeding years each half of the root is again repeatedly split by the death and decay of the cells composing the secondary parenchyma rays between the forking wedges of vessels and sieve-tubes. The formation of well defined annual rings in this species makes it possible to determine that during the winter the vessels and sieve-tubes of a single growing season only are present. The diarch roots of *Aconitum* become divided in almost exactly the same manner as *Corydalis*, except that in the former periderm separates the dead parts from the living. The triarch, tetrarch and pentarch roots of this plant may undergo a primary division into a larger number of parts.

In *Mertensia*, as well as the species described by Jost, the dissection of the subterranean parts into externally separate strands is a result of the removal of the xylem and phloem directly connected with the dead annual parts of the plant. This pruning away of older tissue is, if anything, more severe in *Mertensia* than in any of the other described



plants with dissected rhizomes and roots, for, *at the very outset of any growing season, all but the merest fringe of the products of the cambium during the previous growing season is cut away, and never more than one "annual ring" of active xylem and phloem is preserved.* Although their method of procedure is radically different from that of most other plants, the behavior of herbs with split rhizomes and roots is the same in kind as that of other perennial species which lack this striking peculiarity. The abscission of effete organs and tissues is a phenomenon so common in the plant kingdom and so well known that specific instances of it need hardly be mentioned here [see Skutch (21) pp. 388-89]. As Jost justly remarks, the species described by him stand midway between those perennial herbs which die away at the basal end in measure as they produce new shoots at the apical, and those which preserve and thicken the primary root and rhizome at the same time that they produce new organs. With the latter they have in common the retention of organs, with the former the withering of the oldest tissues. And even in trees which in old age are generally hollow, as the willow, we find a certain analogy to these herbs with dissected rhizomes.

In spite of these points of agreement with other plants with dissected organs, *Mertensia* surpasses in complexity any of the other species we have just discussed. In these the cambium does not close about the inner side of the bundle of vessels left by the dissection of the root or stem, and accordingly no secondary vascular bundles of inverse orientation are ever formed. Although certain portions of the cambium and its derivatives disappear from the scene, the remainder of the cambium ring goes on to produce phloem externally and xylem internally, and behaves, in all essential features, almost as though this interruption of its continuity had never occurred. There is no new formation of cambium, no production of secondary xylem and phloem in abnormal relation to each other. For this reason Pfeiffer (16) denies that these plants exhibit "Abnormal growth in thickness" as defined by him in his monograph of that title. The formation of a closed cambium ring in each strand and the production of bundles of inverse orientation remove *Mertensia* from the category of *Gentiana* and *Corydalis* and place it on a par, anatomically, with the abnormally thickened lianas. A cross-section of the bundle of strands which results from the repeated dissection of a single stem or root of *Mertensia* exhibits a complexity in gross structure equalled only by some of the most advanced climbing stems of the Leguminosæ, Malpighiaceæ, Sapindaceæ, etc. It is of interest to compare our Fig. 10 with Pl. III, fig. 30b, Pl. IV, fig. 42b, and

Pl. X, fig. 130, for example, in Schenck's (20) monograph. The methods by which the structures delineated in these figures arose are in each case different in detail, but the end results are certainly comparable in complexity.

It is impossible to find an exact parallel to the behavior of *Mertensia* among climbing plants because in the latter the formation of secondary vascular bundles is not associated with the dying away of the older tissues. The cable structure which adapts the stems of these plants to the mechanical demands made upon them is secured by the breaking up of the hard xylem into distinct strands imbedded in the softer phloem, without the necessity that these strands be externally distinct; and lianas, just the contrary to *Mertensia*, are characterized by the long-continued efficacy of their conducting elements. In many lianas, however, the stem does at length become divided into externally distinct strands (e. g. *Cassia* among the Leguminosæ and *Sabicea* among the Rubiaceæ [Cruger (3)], *Serjania* among the Sapindaceæ [Schenck (20)]]. *The formation of a dilatation parenchyma in which a cambium arises* is a peculiarity which allies *Mertensia* in the first degree with many lianas, we need mention only *Stigmatophyllon* and *Tetrapteris* (Malpighiaceæ) and *Serjania* [Schenck (20)]. In *Serjania piscatoria*, for example, if we leave aside the irregular arrangement of the primary bundles, and the formation of secondary bundles in the peripheral tissues, and consider only the central xylem mass, we find a certain parallel, albeit of the most general sort, to *Mertensia*. Through the dilatation of the cells of the medullary rays, the sinuses of the originally deeply lobed cambium are prolonged inward until they enter the pith, in the outer portion of which a dilatation tissue is also formed. A cambium ring finally encloses each of the segments, usually four, into which the woody cylinder is split, and produces xylem on the interior of the ring and phloem on the exterior, that is, toward the sinuses and the central pith (see Schenck, Pl. V, fig. 52b).

Since *Mertensia* displays, in common with lianas, a highly developed cable type of structure, it seems not unnatural to look for a common explanation of the evolution of the habit. It is a far cry from the stems of lianas pendent from the boughs of tropical trees to the stems and roots of *Mertensia* buried beneath the stones on arctic and subarctic sea-coasts. Both, however, are subjected to mechanical stresses of kinds not encountered by most other plants. The liana, in the views of Schenck (20) and Haberlandt (7), has developed the cable structure as that best fitted to withstand the torsions, flexures and tugs to which it is



subjected and, if it be a twiner, at the same time adapt itself to the often considerable radial stress it experiences as the tree about which it is coiled grows in diameter. Such a structure, on the other hand, would be impracticable in any plant which depends for its place in the sun upon the rigidity of its own stem. The root or buried shoot of a plant of *Mertensia* growing in shingle must, as it increases in diameter, force aside the stones which surround it for its entire length. The subterranean organs of practically every plant come into contact with occasional stones, but those of *Mertensia* are completely encased in them. Pushing against these stones, they are subjected to considerable and *unequal* radial stresses. The tap-root of *M. virginica*, at home in alluvial loam, would seem to us utterly lost in the stony bed of a sea lungwort. But the latter plant, like the former completely devoid of mechanical elements in its subterranean parts, is able to adapt itself to the irregularities of the stones by flattening out the constituent strands of the cable where need be, as one often discovers on digging up the plant. Furthermore, a local injury inflicted by crushing against the rocks is not so likely to prove serious where an organ is divided into distinct strands, as when it is entire and solid.

We have said nothing about strains to which the plant may be subjected through the shifting of the shingle by the waves, because on Mt. Desert Island we have seen little evidence of its occurrence. As Carey and Oliver (2) have pointed out, the movement of the shingle is entirely confined to the surface layers and, where plants have been buried by the rolling of shingle higher up on the beach, it has been apparently without the disturbance of the strata in which the plant was already established. On other shores, however, it is conceivable that the plants of *Mertensia* may be alternately covered and uncovered, in which case great flexibility, such as is found in the cable type of structure, would be of much service. This point deserves further observation.

Assuming the survival value of the stranded structure of *Mertensia maritima*, and recognizing a foreshadowing of its habit of cutting off the older tissues by periderm in *M. virginica*, which we may take as in this respect a more primitive type of the genus, we could conceivably account for the present structure of the plant by the natural selection of random variations. Opposed to this view is the question of the direct influence of mechanical stresses on the morphology of the plants, the answer to which here, as in the case of lianas, we can hardly surmise.

Another aspect of the problem which deserves consideration is that of size. One thinks of Bower's suggestive paper on "Size, a Neglected

Factor in Stellar Morphology" (1). With the increasing diameter of a solid organ, the aeration and nutrition of its central tissues becomes more difficult. One manner in which the difficulty may be overcome is by the splitting of the organ into distinct strands, as occurs in *Mertensia*. Large size, with the increased possibility of the production of large numbers of seeds by a single individual, is of great value to a species like *Mertensia*, which seems to thrive best on stretches of shore (up-building shingle), where the establishment of seedlings is most hazardous (see above, p. 8). While it might not seem difficult for a small plant of *Mertensia* to overcome the mechanical difficulties of life in the shingle without becoming dissected, it is hard to imagine how a solid, undivided tap-root or rhizome, upright as is the fixed habit of the plant, could become large enough to support at its crown 250 flowering stems, without experiencing great obstacles in making the essential mechanical adjustments to its environment. Then, too, although the shingle is of its very nature a well aerated substratum, it must be remembered that *Mertensia* is provided with no lentecils, and no radially elongated cells forming a true medullary ray, so that the aeration of such a mass of necessarily very active tissue would prove difficult.

Other plants, lacking the habit of *Mertensia* we have just described, exist side by side with it on the shingle. These are plants of different growth forms and different affinities, that started their evolution as shingle beach plants with different structures and different hereditary constitutions, so we can judge little of the value to *Mertensia* of any structure presumably an adaptation by its failure to appear in these others. Here as elsewhere we see that plants with their plastic organization solve the same problem of adaptation to life in a particular habitat in many diverse ways. The sea lungwort's solution is only one of them, perhaps the best possible for a species with its particular phylogenetic background, but of no universal validity.

While working over the anatomy of *Mertensia*, I was interested in seeking evidence of the applicability of the views of Priestley (18, 19) on the rôle of the endodermis in the origin of periderm. Not only do we have the formation of periderm beneath the endodermis of the root and the subterranean portions of the shoot, but also its production in the peripheral portion of the pith of the etiolated shoot, sometimes in the central xylem of the tap-root, and around each strand formed by the dissection of root and stem. Briefly, Priestley holds that it is the accumulation of solutes behind the relatively impermeable barrier which the endodermis forms, especially after its tangential walls have become



suberized, or it has entered the "secondary stage," to use his own terminology, which is responsible for the beginning of meristematic activity in the pericycle. We saw that in both the hypocotyl and the etiolated shoot the endodermis had entered the secondary stage at the time of the first phellogenic divisions in the pericycle. In the pith of the etiolated shoot also, the suberization of a layer of cells near its periphery was accompanied by the origin of a phellogen in the next layer exterior to it, that is toward the vascular tissue and the course of the solutes carried down from the leaves. In the aerial stem the endodermis remains in the primary stage, its tangential walls do not become suberized, and in the pith the walls of the layer of cells corresponding to those which become suberized in the etiolated stem remain unsuberized. Here no phellogen is formed, either in the pericycle or in the pith. We have also seen that in the dissection of the subterranean organs the walls of a layer of cells surrounding each new strand become suberized before a definite phellogen is formed. There is a possibility that some decrease in the permeability of the cells of this layer occurred even before the origin of the dilatation parenchyma and was responsible for it, but this point was not specifically investigated. In another suggestive paper, Priestley (17) states that there is much evidence for the view that "the main morphological and structural features of etiolation are determined by a redistribution of growth at the shoot apex, consequent upon the greater difficulty experienced by the meristem in drawing nourishment from the vascular supply because, when growing in the dark, the walls between vascular strands and meristem are rendered relatively impermeable by the retention in them of the protein and fatty substances that form the surface of the protoplast." Probably it is a similar difficulty in drawing nourishment from the vascular strands that is responsible for the cutting out of the pith of the etiolated shoot of *Mertensia*—the fatty substances accumulate in a layer relatively near the vascular bundles, with the result that a periderm arises in the next layer to the exterior. And we can only surmise how far the difficulty of obtaining nourishment at a distance from the *active* vascular elements is responsible for the whole process of dissection as we have described it in *Mertensia*.

#### SUMMARY

1. *Mertensia maritima*, an herbaceous plant of high northern latitudes of both hemispheres, grows on shingle and sandy beaches. The shingle bar, with its peculiar restrictions as to soil and water, forms a favored habitat.

2. On Mt. Desert Island, Maine, the seeds germinate about the first week of June. As a result of the dimness of light in the shingle in which they germinate, most of the seedlings show the typical aspect of etiolation. Seedling mortality is very high.
3. The root and the lower portion of the hypocotyl are exarch and diarch. Only in its upper quarter does the hypocotyl contain a pith.
4. The hypocotyl and primary root of the seedling develop into a fleshy tap-root, which during the first summer bears a rosette of leaves at its crown.
5. No fibres are formed in the secondary xylem or phloem of the root. The vessels and sieve-tubes occur only in sectors which alternate with broad parenchyma rays. These sectors fork repeatedly.
6. By the middle of August, the cambium has become relatively or completely inactive where it crosses the parenchyma rays. The oil globules, which are the principal food reserve of the plant, disappear from these rays and from the outer secondary cortex.
7. During the first summer, the central xylem of the tap-root is sometimes cut off from the younger tissue by a periderm, and then it disintegrates. The cambium is produced inward along the edges of the primary parenchyma rays, and sometimes forms a closed ring around each of the two masses of remaining secondary xylem. By the extension of the central periderm along the primary parenchyma rays until it meets the outer periderm surrounding the organ, the tap-root and some of the most vigorous lateral roots are split in two. This form of fission is of sporadic occurrence.
8. In the spring of the second year the cambium produces a number of very wide vessels which contrast sharply with the narrow vessels formed at the end of the preceding growing season. As a result of the return to the meristematic state of the parenchyma cells between the latter, a dilatation parenchyma is formed.
9. The newly formed xylem and phloem of a single wedge, or of a group of adjacent ones together, is cut off by periderm from all of the older tissue. In the xylem, the periderm arises at the inner edge of the dilatation parenchyma.
10. The cambium is produced inward around the edges of each group of spring vessels and across the dilatation parenchyma, forming a closed ring around the newly produced xylem of each sector of vessels, or group of adjacent ones.



11. By the decay of the older tissue cut off by the periderm, the tap-root becomes divided into longitudinal halves, each of which is a network of anastomosing strands.
12. The intraxylary cambium of the stronger strands originates new vascular bundles of inverted orientation in respect to the organ in its entirety.
13. In the following spring the newly formed xylem and phloem of each wedge in the primary strand is isolated by periderm to form secondary strands. This process is repeated year after year until a thick cable of strands is formed.
14. In its second year the perennating tap-root sends out decumbent aerial flowering shoots. These die off in the autumn, but are renewed in the following year from the mass of dormant buds which arises at the crown of the tap-root.
15. When a plant which has been buried beneath the shingle during the winter storms becomes active again in the spring, it sends out shoots which push up through the overlying stones and show the usual symptoms of etiolation. The portions of these shoots buried in the shingle, differing fundamentally from the aerial portions in their anatomy, constitute an addition to the perennating portion of the plant.
16. There are five common and five cauline bundles. At the apex of the shoot the common bundles contain several times as many differentiated xylem elements as the cauline. After the beginning of cambial activity the cauline bundles are very considerably thickened by the formation of numerous conducting elements, while practically none are added to the common bundles. The cambium of the common bundles has generally become inactive by the middle of August, at a time when that of the cauline bundles is still actively dividing. This difference in the behavior of the two classes of bundles is of the utmost importance in determining the future structure of the stem.
17. In the etiolated portion of the shoot, there is a reduction of the number of distinct bundles to six, five or rarely four, although the phyllotaxy does not change.
18. In the etiolated portion of the shoot, the endodermis enters the secondary stage and a periderm, arising beneath it, cuts off the cortex. At the same time, the pith is cut off from the vascular tissue by a periderm which originates outside of a layer of medullary cells which become suberized.

19. In the following spring, the newly formed xylem and phloem of the cauline bundles is separated by a periderm from all surrounding tissue. With the decay of the older tissue, these form externally distinct strands, the course of which is determined by the primary arrangement of bundles in the stem. Only those cauline bundles which lead to actively growing lateral buds are preserved.
20. The subsequent behavior of each strand resulting from the dissection of the stem closely resembles that described for the root. It is not possible by an examination of the cross-section to distinguish one from the other.
21. In *Mertensia virginica* we find a foreshadowing of the behavior described for *M. maritima*.
22. *Mertensia maritima* far surpasses in complexity any hitherto described herbaceous plant with split rhizomes and roots. The complexity in form of the cable of strands resulting from the repeated dissection of a single axial organ finds a parallel only in the stems of certain highly specialized lianas.
23. As in the case of lianas, the cable-like structure of *Mertensia* seems to be an adaptation to the peculiar stresses, not encountered by the great majority of plants, to which its mode of life subjects it. Specifically, these stresses are found in the unequally distributed pressure of the stones in which it grows.
24. The habit of fission also permits the attainment of a larger size than would seem possible in the absence of this habit. Since the establishment of seedlings is so difficult, the large size and the consequent great seed production by the individual is at a premium.
25. The views of Priestley on the rôle of the endodermis in cork formation, and on the distribution of growth in etiolated shoots, find confirmation in the present study.

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FIG. 1.—The shingle bar south of Manset, Mt. Desert Island, Maine. Seven plants of *Mertensia* are growing in the field of view, near the top of the bar. The *Triglochin maritima* marsh which lies behind the beach may be seen at the extreme left.



FIG. 2.—A vigorous plant, about 3 years old, dug up and photographed June 11, 1928. The ruler beneath the tap-root is 30 cm. long. This plant, which had been buried 8 cm. by the shingle since its establishment, bore 260 stems.





FIG. 3.—The plant shown in Pl. 1, fig. 2, *in situ* in the area included in Pl. 1, fig. 1. The ruler in the foreground is 30 cm. long, and the decumbent stems, although not yet full grown, covered an area 120 cm. in diameter.



FIG. 4.—Young shoots of a plant, covered by shingle during the previous winter, growing up through the shingle and mixed debris on a beach south of Manset, June 11, 1928.



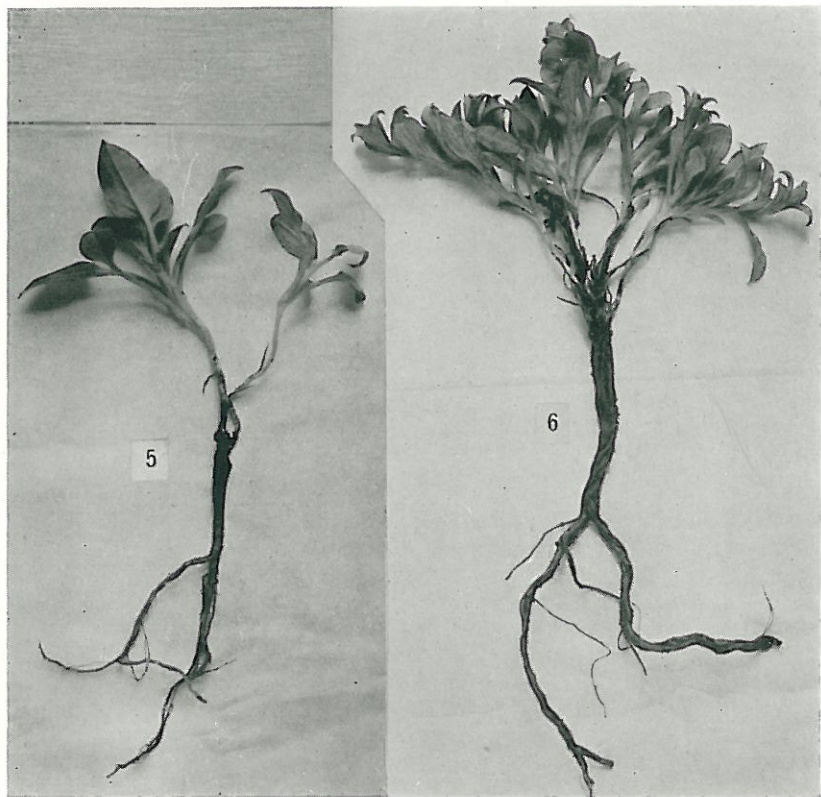


FIG. 5.—A one-year-old plant which had been slightly buried during the preceding winter. Notice the shrunk condition of the tap-root. Photographed June 8, 1928. ( $\times$  about  $1/3$ .)

FIG. 6.—A two-year-old plant which has undergone one period of fission, photographed on June 8, 1928. ( $\times$  about  $1/4$ .)



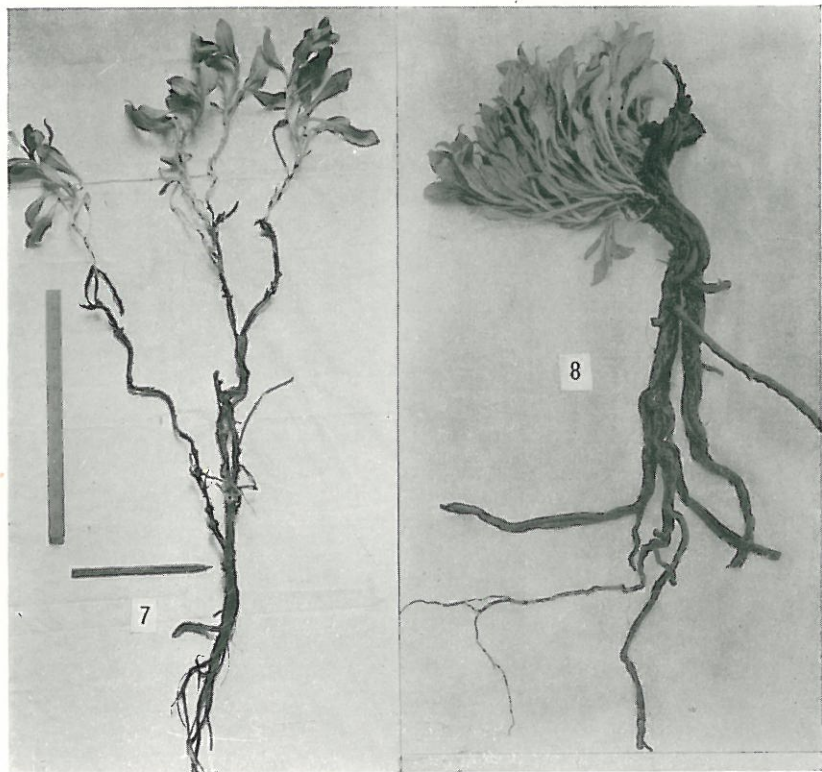


FIG. 7.—A four-year-old plant which had been buried each winter, so that at the time it was dug up the collet was 40 cm. beneath the surface. The pencil points to the collet, the ruler is 30 cm. long. Compare this plant with the much larger plant shown in Plate I, fig. 2, which is a year younger, but had not been so deeply buried. Photographed June 5, 1928.

FIG. 8.—A plant which had been buried by the shingle and was uncovered again during the winter before the picture was taken. The new shoots arise from near the base of an old, several-times dissected stem. Photographed June 5, 1928 ( $\times$  about 1/5).



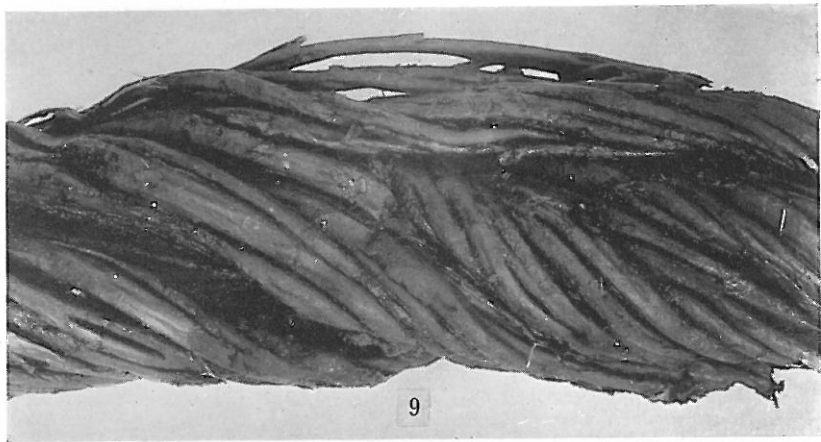


FIG. 9.—A several-times-dissected root collected August 19, 1925. At one cross-section of this root 60 distinct strands were counted. Notice the spiral trend of the strands ( $\times$  about 2).

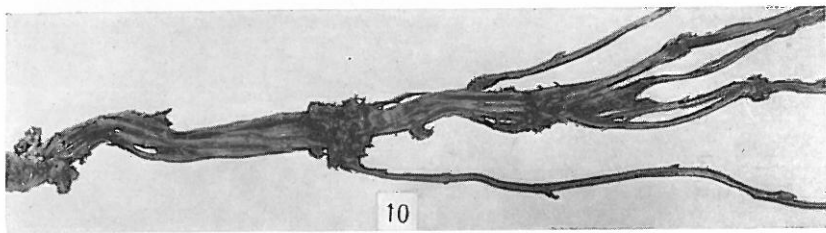


FIG. 10.—A dissected stem with its branches, to show the swollen masses of dormant buds at some of the nodes. Collected August 19, 1925 ( $\times$  about  $1/2$ ).

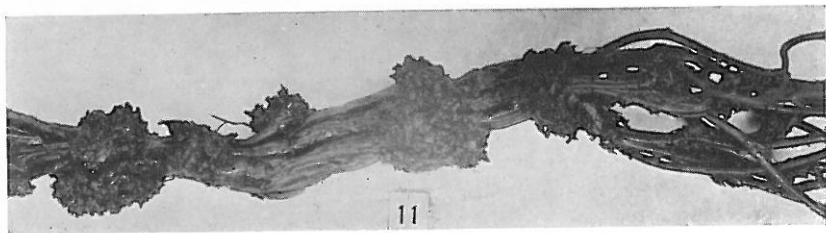


FIG. 11.—Another stem like that shown in Fig. 10. ( $\times$  about  $1/2$ ).





FIG. 15.—The tap-root of a plant in its fourth summer. Text-fig. 10, a cross-section made of the same hypocotyl after it had been photographed, shows that it had been dissected on three separate occasions and consisted, at the level of this figure, of 74 distinct strands. Notice the massed buds at the crown. Collected August 19, 1928. ( $\times$  about 1.2.)

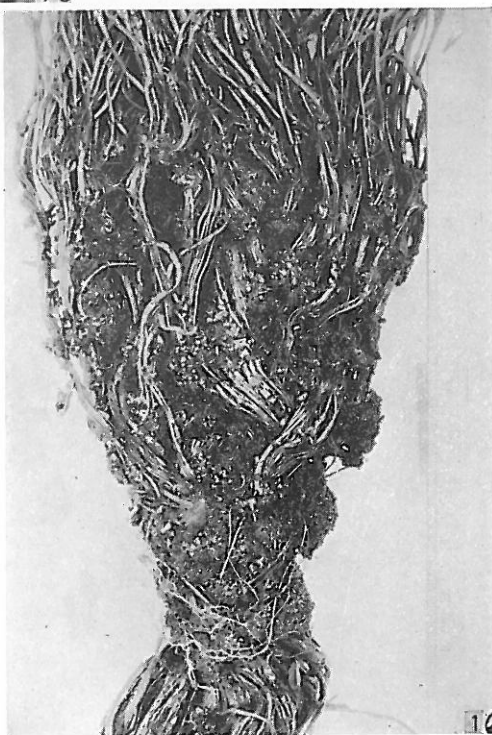


FIG. 16.—The perennating bases of the stems of a four or five-year-old plant growing on the shingle bar at Bass Harbor (see text, p. 6). These stems have together been dissected into hundreds of strands. The tap-root is shown at the very bottom of the figure, and the bases of the flowering stems of the present season are clustered at the top. The depth of burial of this plant since its establishment was about 30 cm. The ruler at the right is 12 inches long. Collected August 19, 1925.



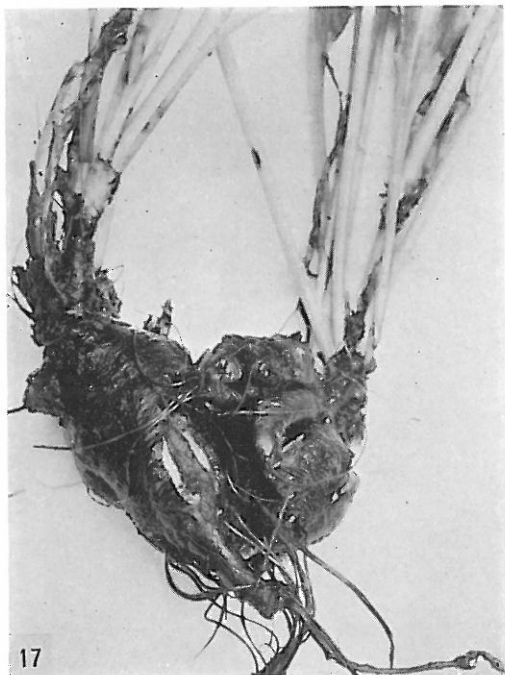


FIG. 17.—The basal portion of a plant of *M. virginica* collected in Baltimore County, Maryland, May 22, 1928. A split in the outer secondary cortex of the root, which is being cut off from the living tissues by periderm, is plainly visible. ( $\times$  about 1).

FIG. 18.—A cross-section of the buried base of a shoot of *M. maritima* in its first summer. For explanation see text pp. 30, 31, 33. ( $\times$  about 25.)

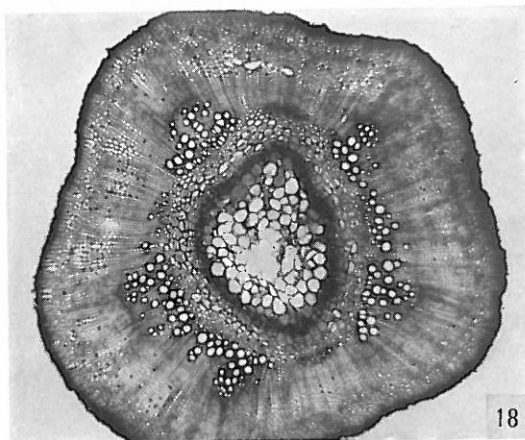


FIG. 19.—A halved root of *M. virginica*, showing the internal cavity. The periderm which cuts off the outer secondary cortex is plainly visible in the figure; that cutting out the oldest extant xylem is not so distinct. Collected May 22, 1928 ( $\times$  about 2/5).

