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THE SHOOT APEX OF *CALLISTOPHYTON POROXYLOIDES*

BY

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UNIVERSITY OF MICHIGAN
ANN ARBOR

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INTRODUCTION

DISCOVERY of a fossil plant of previously unknown type is often followed by the immediate recognition of many similar forms. Such has been the case with *Callistophyton poroxyloides,* which was first described by Delevoryas and Morgan in 1954. Since the publication of that report, stem fragments of the species have been found in coal balls from Berryville, Calhoun, and Dix, Illinois, and closely similar forms were collected from southeastern Kansas. The coal balls from the Illinois localities came from the Upper McLeansboro group of the Pennsylvanian period, whereas those from Kansas originated in the Fleming coal, Cherokee shale, of the Des Moines series, also Pennsylvanian in age.

The specimen of this report came from a creek bed near Berryville in Lawrence County, Illinois. It is the apical part of a stem and includes the very tip of the plant. Since tissues in plant apices are thin-walled, they almost invariably disintegrate or decay early in the process of petrifaction. As a result, fossilized apices are rather rare and any in specimens collected are of considerable interest. This particular apex is significant because the

* This project was completed while the author was a Rockefeller Fellow in the Natural Sciences of the National Research Council. The author is grateful to Professor W. N. Stewart, Department of Botany, University of Illinois, for loan of the material for study. He also wishes to thank Professor R. V. Kesling of the Museum of Paleontology for advice concerning the preparation of plates.

internodes are telescoped, so that several nodes occur on a short length of stem. Furthermore, since the lateral appendages are not fully expanded, a relatively large part of them can be observed. Mature structures are so large that they are usually fragmentary when preserved.

All sections are transverse and were made by the nitrocellulose peel technique as modified by Darrah (1936). Slides are deposited in the Department of Botany, University of Illinois, and the Museum of Paleontology, University of Michigan.

HISTOLOGICAL DETAILS

A conspicuous feature of this young stem and of the attached leaves is the dense covering of multicellular hairs (see Plate I). These dermal appendages are of two types: some are long slender hairs which average 20μ in diameter and may be one or more cells thick and up to 2 mm. long.; the others are stouter with swollen, apparently glandular tips very much like the hairs figured by Delevoryas and Morgan (1954, Pl. 12, Fig. 17). Longitudinal strands of sclerenchyma surround the parenchyma of the inner cortex at the periphery of the cortex. The cortex contains numerous large, spherical secretory cavities, which may be as large as 0.3 mm. in diameter. Some of the cavities are filled with amber-colored remains (see Pl. I, Figs. 1–2). At this immature stage there is no periderm layer; it apparently formed within the cortex as the stem became older (Delevoryas and Morgan, 1954, Pl. II, Fig. 13).

All that can be recognized of mature vascular tissue are small isolated patches of primary xylem. Secondary vascular tissue is absent; the stelar pattern is marked primarily by the cylinder of procambium. The procambium stands out from the outer cortical cells and the inner pith cells because of the narrow diameter of its elements. In the illustrations it is conspicuous because of the darker shade. Immediately surrounding the procambium there are many cells which look as if they were thick-walled. In a transverse section of the stem they look very much like tracheids, but they are not elongated and probably also had a secretory function. These cells are absent in the older stages of the stem, but that is probably due to their obliteration by the secondary vascular tissue. The pith is entirely parenchymatous with a few secretory cavities.

COMPARISON WITH OLDER STAGES

Since the original description of the species deals only with stems having secondary vascular tissue and showing no transition to the younger, apical parts, the reasons for identifying the new material as *Callistophyton*

poroxyloides need to be listed. The surface of the young stem and the leaves is covered with a dense mass of hairs of two types. Most of the hairs were probably lost as that part of the stem grew older and only the larger ones, with the expanded tips, persisted. This type of pubescence is found in older stages. The vertically extending strands of sclerenchyma, just beneath the epidermis, are reminiscent of a similar feature in the older ones. Secretory cavities in the pith, cortex, and leaf rachises, four protoxylem groups that enter each leaf base, and axillary branching (except for a few instances of adventitious budding in some older stems) occur in the young and older stages. In both, the petioles are tangentially expanded, with a single flat, or slightly curved trace within each one and the leaves are frondlike. With so many features in common, it is quite evident that the shoot apex is conspecific with the older specimens.

ANATOMICAL OBSERVATIONS

No longitudinal sections were made because only one specimen in which the apical region was preserved was available. Besides, the general structure of the shoot apex and the leaf structure and arrangement could be determined from a series of transverse sections. In the small fragment of stem, about 1.5 cm., eight leaves or leaf primordia originate. The observations given below are taken from a series of peels that are arranged in ascending order from lowest to highest level.

1. Base of specimen has diameter of 5.2 by 3 mm. (Pl. I, Fig. 1). This section is just below the level of separation of a leaf.

2. Procambium is extended into leaf base; potential leaf trace not yet separated from procambium of stem (Pl. I, Fig. 2).

3. Base of first leaf clearly delimited; gap in procambium marks area of separation of trace (Pl. I, Fig. 3).

4. First leaf base now free (at left in figure); gap in procambium completely closed (Pl. I, Fig. 4). The origin of the petiole, at right, was below the base of the specimen; it was not seen attached in the coal ball (count of leaves does not include this one).

5. Two patches of sclerenchyma projecting inward, at lower right, indicate position of next leaf in sequence; its trace has just separated from stem procambium (Pl. II, Fig. 1).

6. Second leaf base almost free of stem; two curved strands, on either side of leaf gap, represent trace of an axillary bud (Pl. II, Fig. 2; Fig. 2).

7. Base of second leaf separated; axillary bud evident; four small strands of protoxylem mark trace of third leaf (Pl. II, Fig. 3).

8. Transverse section shows two leaf primordia of axillary bud (Pl. III, Fig. 1).

9. Third leaf base almost free from stem, upper part of figure (Pl. III, Fig. 2).

10. Position of origin of fourth leaf base evident, lower part of figure (Pl. III, Fig. 3).

11. Fourth leaf base completely free; origin of fifth leaf base seen, upper right (Pl. IV, Fig. 1).

12. Procambium is divided to supply fifth and sixth leaves (Pl. IV, Fig. 2).

13. Sixth leaf base (Pl. IV, Fig. 3). The sixth leaf appears to precede the fifth because section is slightly oblique.

14. Origin of seventh leaf base, (below in Pl. IV, Fig. 3) and eighth leaf base (above, same plate and figure). Both bases seen more clearly in the highest level of the stem (Pl. V, Fig. 1). Only a small part of the stem apex is evident between the primordia of the seventh and eighth leaves. Because of the delicate nature of the cells in the apex, preservation is not sharp enough to reveal information concerning the cellular arrangement in the tip. Knowing whether an apical cell or a multicellular apical meristem was present would help in determining the phyletic position of some of the monostelic pteridosperms.

LEAF STRUCTURES

In the original report, sections of petioles, pinnae, and pinnules are described and figured. Although not all of the component parts were associated, the authors were able to discern the frondlike structure through observation of pinnae attached to petioles and pinnules attached to other pinnae of identical structure. The new material not only confirms the frondlike nature of *Callistophyton* leaves but it further shows that their vernation was circinate.

Just above the point at which it separates from the stem, a petiole is somewhat crescent-shaped, with the concavity on the adaxial side (Pl. III, Fig. 1). At higher levels (Pl. V, Fig. 3) this concavity disappears or is even replaced by a bulge, so that the rachis is more nearly cylindrical. This configuration may change in the older stages, for all petioles observed by Delevoryas and Morgan were tangentially expanded. In the lower part of the undeveloped leaves, the xylem in the petiole trace consists of four protoxylem groups; these divide a little higher. The traces to pinnae arise from the edges of the petiolar vascular strand, one trace supplying each pinna. Primary pinnae are attached obliquely so that at the lowest level

at which a pinna base is first recognizable, it appears as a bulge on the edge of the petiole (Pl. IV, Fig. 1). The pinna becomes completely free from the petiole at higher levels (Pl. IV, Figs. 2, 3; Pl. V, Figs. 1, 2). Primary pinna pairs do not arise at quite the same level; hence, their arrangement, at least in this young stage of development, may best be described as subopposite.

Secondary pinnae arise in two ranks along the edges of the primary pinnae and, because of the circinate nature of the fronds near the apex,

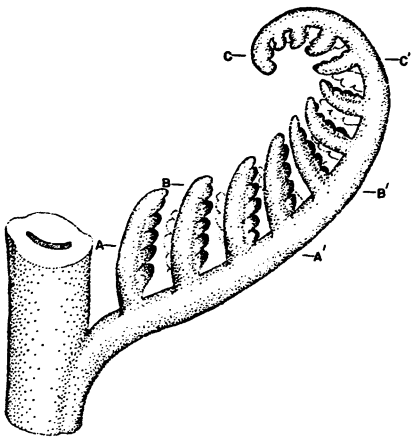
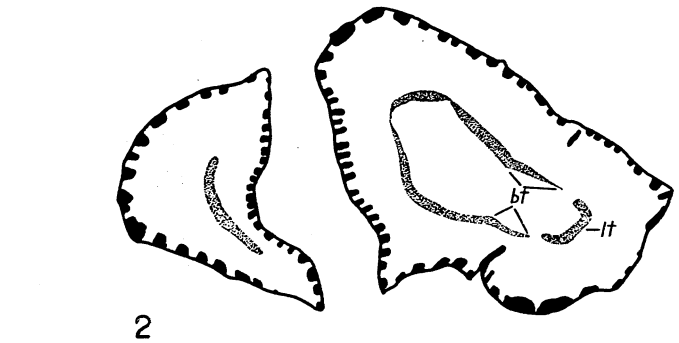


FIG. 1. Reconstruction of part of a developing frond of *Callistophyton poroxyloides;* circinately coiled primary pinna is attached to a segment of the petiole. Plane A-A′ corresponds to Plate V, Figure 3 (lower left); B-B′ to Plate VI, Figure 1; and C-C′ to Plate VI, Figure 3 (lower part).

appear to arise at right angles to the longer cross-sectional axis of the primary pinna (Pl. V, Fig. 3). The sectional configurations of the primary and secondary pinnae in the lower part (Pl. V, Fig. 3; Pl. VI, Figs. 1, 2) can best be interpreted by referring to the diagram in Figure 1. In Plate VI, Figure 2, part of a circinately curved pinna (in longitudinal section) can be seen arising from the lower side of the petiole.

Lobations along the edge of the secondary pinnae in the lower leaves in the specimen probably represent pinnule primordia. In Plate V, Figure 3 (see lower part of photograph) they are visible as slender curved structures; none are far enough developed to be seen on the secondary pinnae of higher leaves. If these structures are the pinnules, the leaves of *C. poroxyloides* must have been at least three times compound.



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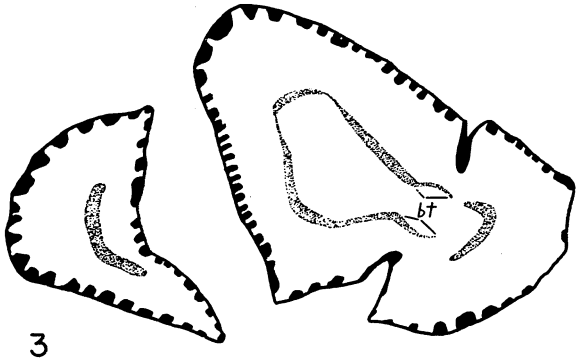

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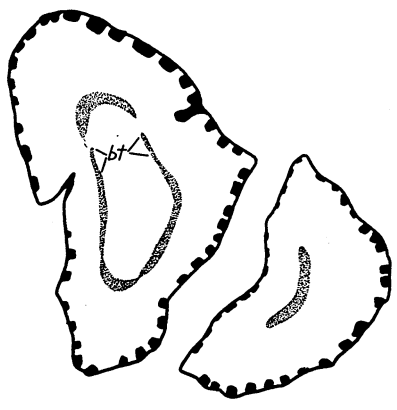

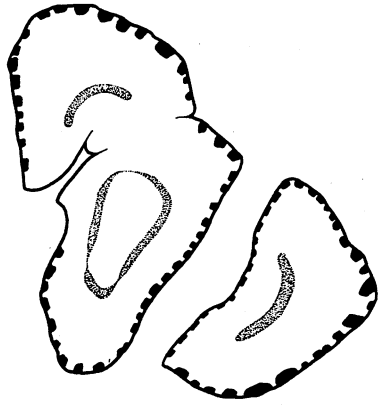

4 5

FIGS. 2–5. Ascending series of diagrammatic transverse sections showing bud-trace formation. See text for full explanation. lt=leaf trace; bt=bud trace. Figure 2 is drawn from C. B. 1160 d top 16 (Pl. II, Fig. 1); Figure 3, from C. B. 1160 d top 19 (Pl. II, Fig. 2); Figure 4, from C. B. 1160 d(1) top 35; and Figure 5, from C. B. 1160 d(1) top 37 (Pl. II, Fig. 3). For explanation of formula, see Plates, Note 1.

AXILLARY BUDS

A bud is situated in the axil of one of the leaves (Pl. II, Fig. 3). Although other buds are not apparent in the higher sections, they were, no doubt, present in the axils of the leaves. Figure 2 corresponds to Plate II, Figure 1. It illustrates a cross section of the stem with a free leaf trace (at lower right) and a bud trace that is still attached to the stelar procambium on either side of the leaf gap. In Figure 3, corresponding to Plate II, Figure 2. the two arcs of procambium representing the bud vascular supply are quite prominent. Plate II, Figure 3 shows the bud still attached to the adaxial face of the petiole base and only two of the primordial leaves on the axillary member are visible in the section in Plate III, Figure 1. The drawing in Figure 4 shows the free leaf trace of the next higher leaf, with two slender strands of procambium on either side of the gap probably representing the bud vascular supply. At a slightly higher level (Fig. 5) there is no evidence of the bud trace, but a small bulge between leaf and stem is all that can be seen of the bud. Above this level, because of the still undifferentiated nature of the structures so close to the apex, other buds do not project out of the leaf axils far enough to be visible in a transverse section.

There is some discrepancy between the structure and method of departure of the axillary branch observed in this young stem and that reported for axillary branching for the species by Delevoryas and Morgan. In their paper it was suggested that the branches did not arise until some distance above the subtending leaf and, furthermore, that a relatively large part of the primary vascular structure of the stem became incorporated in the branch traces. Some of the difficulty can be cleared up if one realizes that the new material is from the very tip of the plant, and is not, therefore, fully expanded. A certain amount of elongation could well have occurred a little later in the ontogeny of the stem. This could easily have taken place, for in the young stem only some of the first-formed primary xylem elements of the mature vascular tissue are evident, and any elongation that occurred would have taken place before the later, more rigid, xylem elements formed and before the peripheral sclerenchyma became fully lignified. Increase in the girth of the stem could also have effected a different ratio in size of bud trace and stem stele than that in the apex of the stem. There was an actual increase in stem diameter, as may be seen from a comparison of Plate IV, Figure 1, and Plate I, Figure 1.

In both this young stem fragment and in the older ones previously described, the pattern of axillary branch development is the same; that is,

a part of the primary vascular tissue on either side of the leaf gap contributes to the formation of the branch trace.

DISCUSSION

As yet the fructifications and roots of *Callistophyton poroxyloides* are unknown. Until seeds and microsporangiate organs of the plant are available, its inclusion in the Pteridospermae must remain provisional. The vegetative structures known, however, are definitely pteridospermous in nature and, if fructifications are found, they will probably serve merely to support the placing of *Callistophyton* with the pteridosperms.

The discovery of *C. poroxyloides* and, in particular, of frond rachises belonging to it, contributes toward the clarification of the affinities of the rachises grouped within the organ genus *Lyginorachis* Kidston (1923, pp. 18–19). In *Lyginorachis* are included petioles which are similar in many respects to those of *Lyginopteris* but cannot definitely be assigned to it. *Lyginorachis Taitiana* (Crookall, 1931, Pl. I, Fig. 1; Calder, 1935, Text-fig. 1, Pl. I, Figs. 10–12) resembles petioles of *Callistophyton poroxyloides* perhaps even more than it does those of *Lyginopteris*. In *Lyginorachis Taitiana* there is a system of hypodermal fibers surrounding a parenchymatous ground tissue lacking in sclerotic nests. There is a single large vascular bundle, which is somewhat U-shaped in transverse section, many patches of protoxylem, and metaxylem that is both centrifugal and centripetal. Calder (1935, Fig. 1) illustrated a descending series of transverse sections of the type specimen of *L. Taitiana,* and each pinna is supplied with a single strand originating from one of the edges of the petiole trace. All these features of *L. Taitiana* are identical with those of *C. poroxyloides* except that the petiole trace in *Callistophyton* is not as conspicuously curved. Another possible point of difference is the arrangement of sclerenchyma strands. Crookall (1931) believed that the appearance of the strands in transverse section "suggests a dictyoxylon structure," since there is some lateral fusion. Lateral fusion does not, however, have to point to a dictyoxylon structure, because fusion occurs in *Myeloxylon,* the petiole of *Medullosa,* which has a different type of sclerenchyma pattern.

The author does not suggest that *Lyginorachis Taitiana* is the petiole of *C. poroxyloides,* but the two have so many characters in common that an additional plant type, besides *Lyginopteris* and *Heterangium,* which Scott suggested (1923), might possibly have been the source of the petioles.

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PLATES

A series of transverse sections of an apical shoot of *Callistophyton poroxyloides,* from the lower part of the specimen to the tip. Figured slides catalogued and deposited in the Paleobotanical Collections, Department of Botany, University of Illinois All photographs ×10.

EXPLANATION OF PLATE I

FIG. 1. C. B. 1160 c(1) bottom 41.[1]
FIG. 2. C. B. 1160 c(1) bottom 29.
FIG. 3. C. B. 1160 c bottom 8.
FIG. 4. C. B. 1160 d top 7.

[1] Formula indicates that the slide was made from the 41st peel from the bottom surface of piece c(1) of Coal Ball No. 1160.

PLATE I

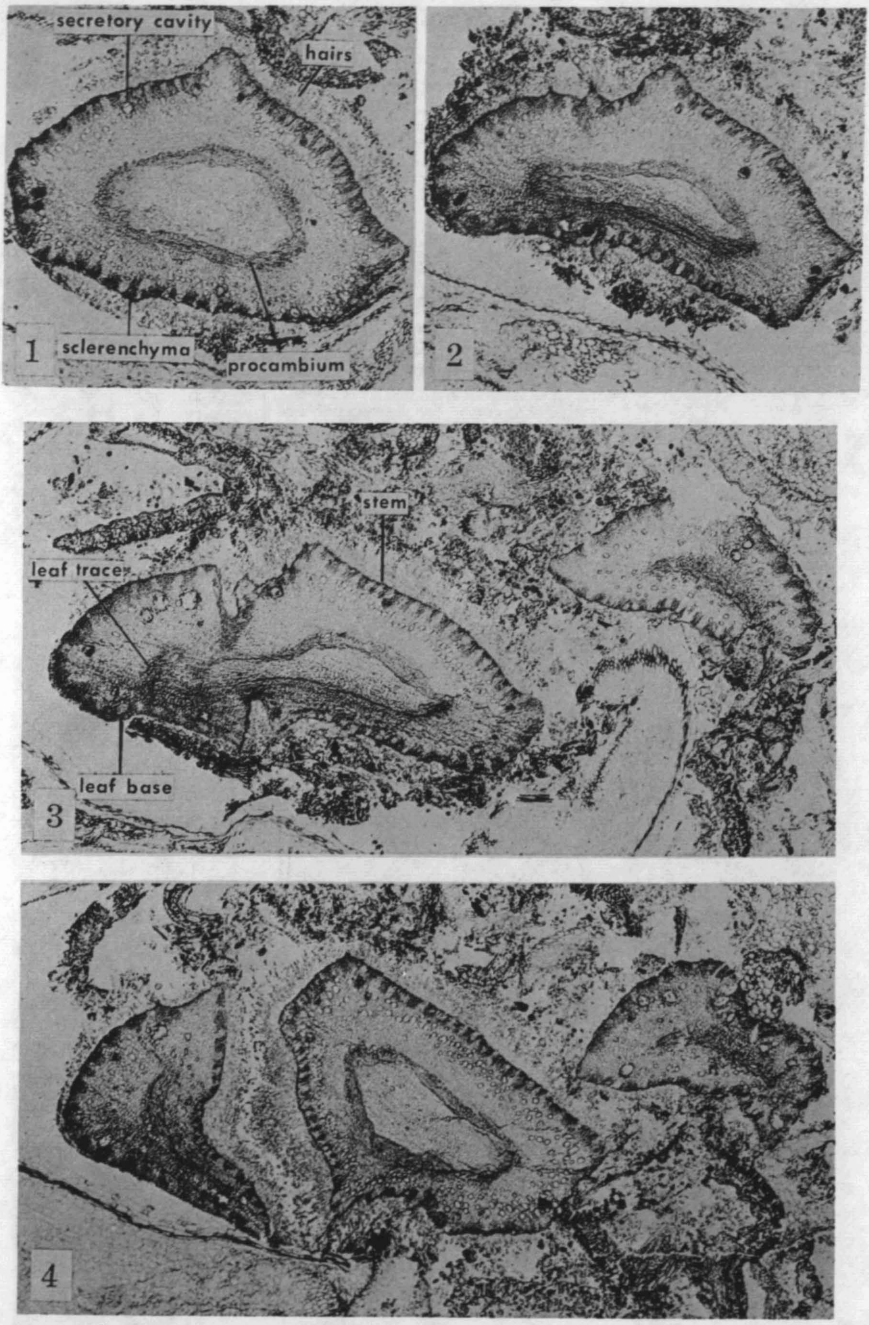
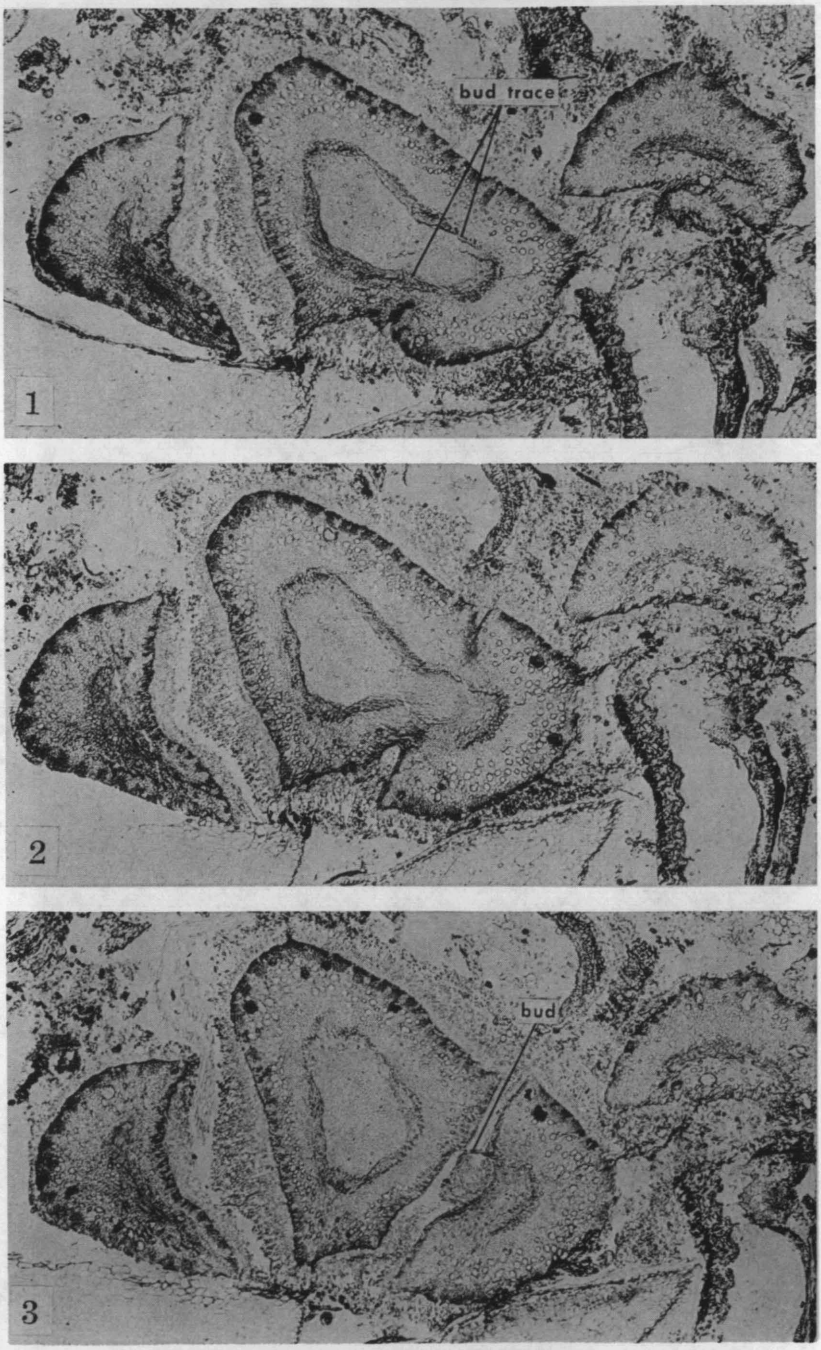

secretory cavity
hairs
1
sclerenchyma
procambium
2
stem
leaf trace
leaf base
3
4

PLATE II



EXPLANATION OF PLATE II

FIG. 1. C. B. 1160 d top 16.[2]
FIG. 2. C. B. 1160 d top 19.
FIG. 3. C.B. 1160 d(1) top 28.

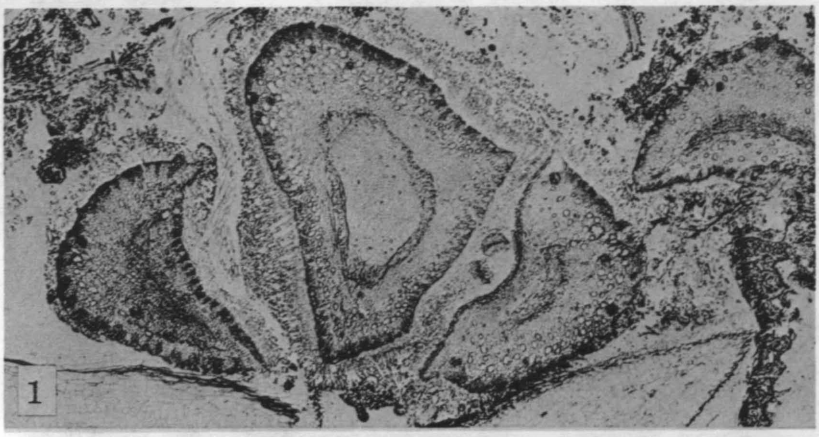
[2] See Note, Plate 1.

EXPLANATION OF PLATE III

FIG. 1. C. B. 1160 d(1) top 31.[2]
FIG. 2. C. B. 1160 d(1) top 37.
FIG. 3. C. B. 1160 d(1) top 43.

[2] See Note, Plate 1.

PLATE III



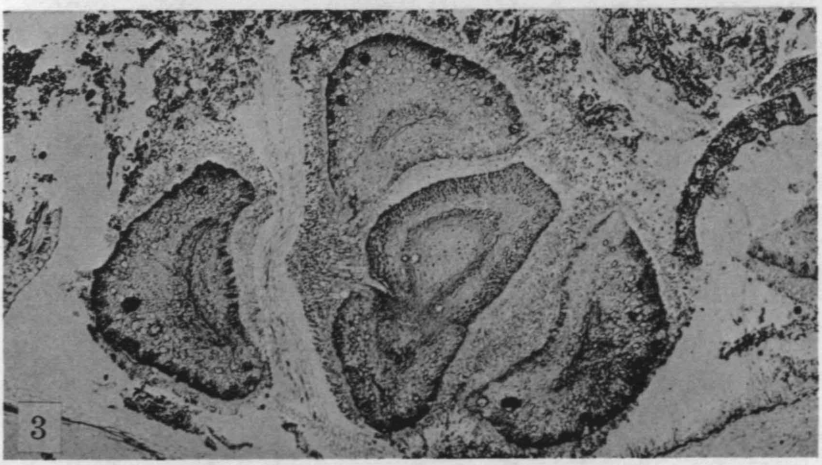
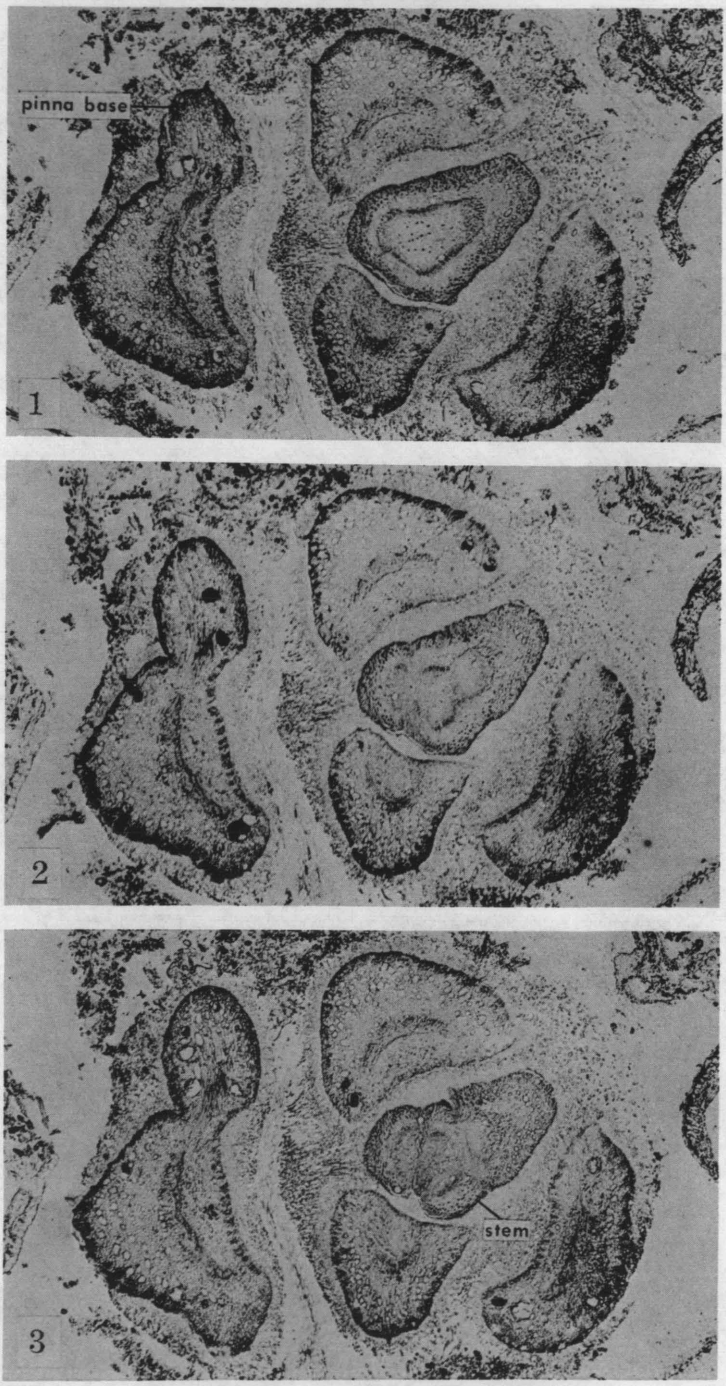


PLATE IV



EXPLANATION OF PLATE IV

FIG. 1. C. B. 1160 d(1) top 46.[2]
FIG. 2. C. B. 1160 d(1) top 47.
FIG. 3. C. B. 1160 d(1) top 48.

[2] See Note, Plate 1.

EXPLANATION OF PLATE V

FIG. 1. C. B. 1160 d(1) top 50.[2]
FIG. 2. C. B. 1160 d(1) top 57.
FIG. 3. C. B. 1160 d(1) top 70.

[2] See Note, Plate 1.

PLATE V

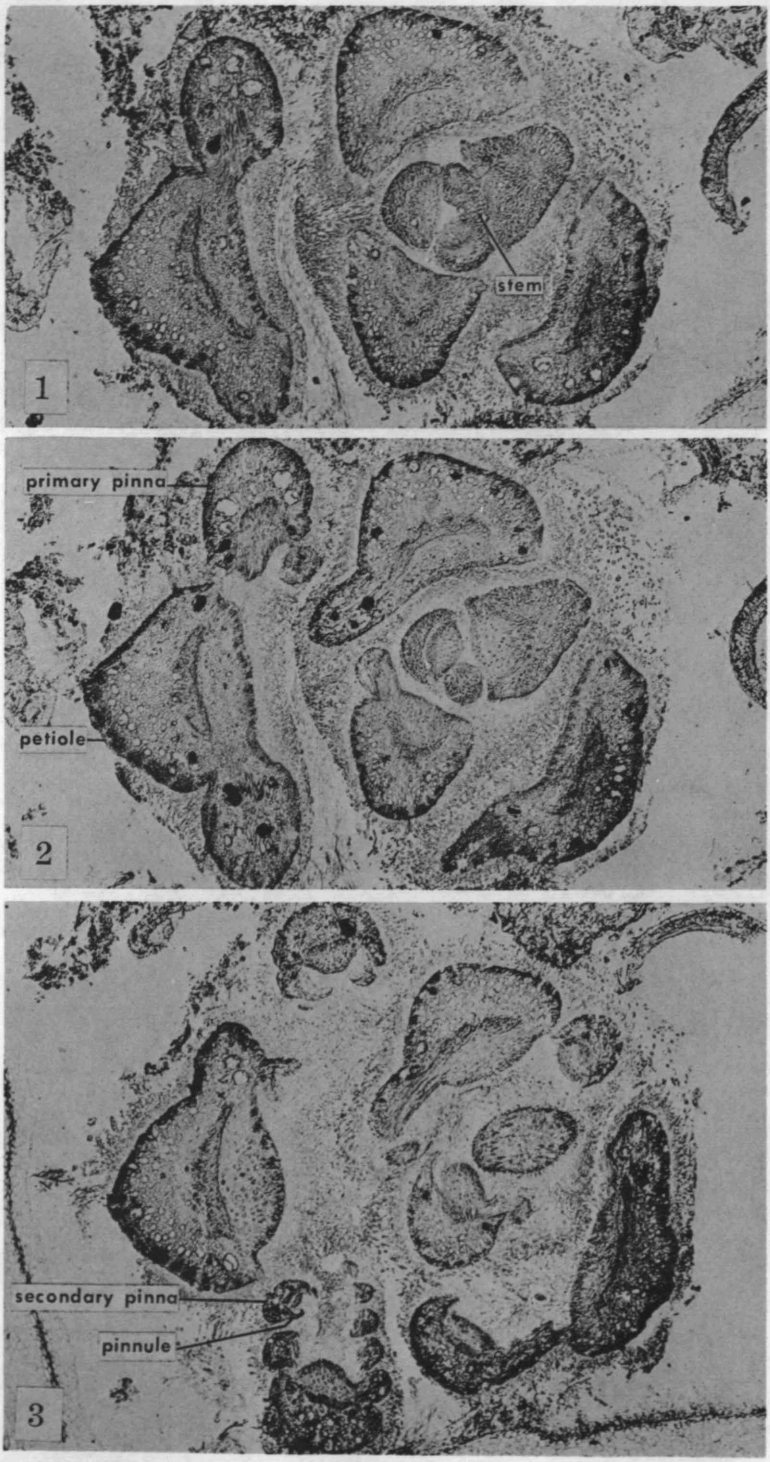
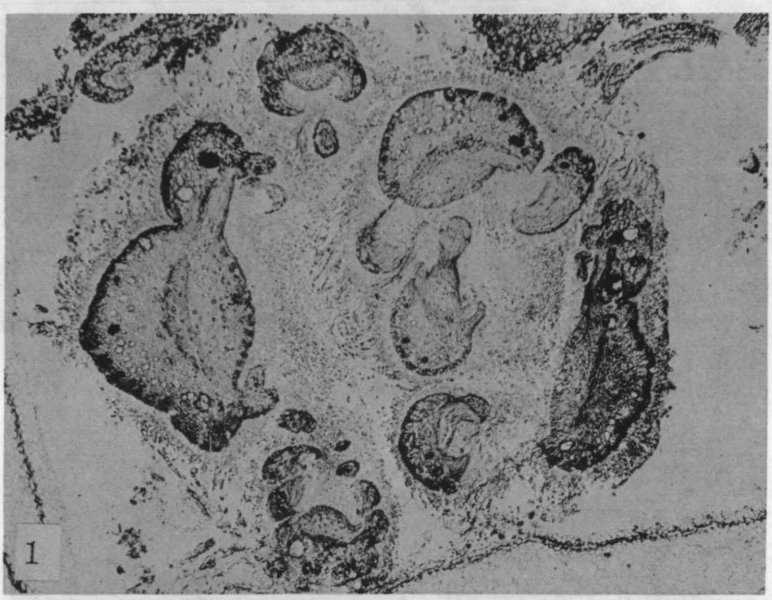
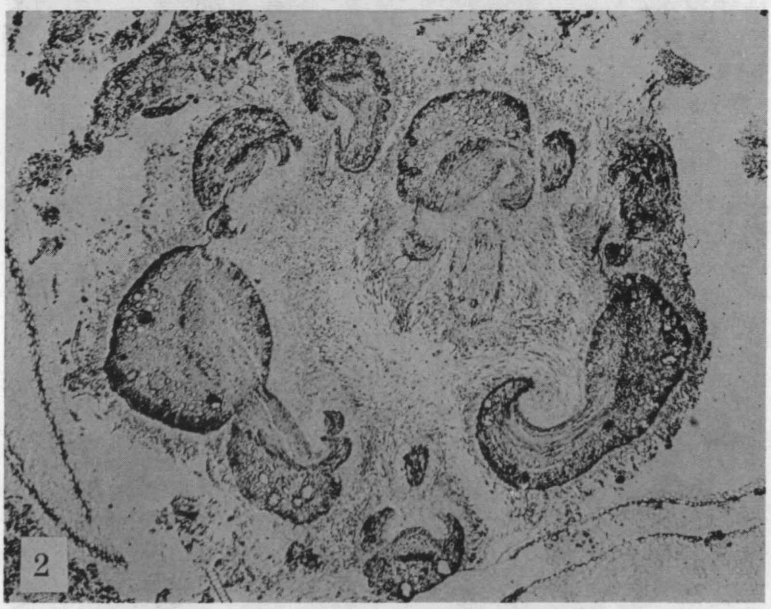


PLATE VI





EXPLANATION OF PLATE VI

FIG. 1. C. B. 1160 d(1) top 72.[2]
FIG. 2. C. B. 1160 d(1) top 77.

[2] See Note, Plate 1.