MORPHOLOGY OF THISMIA AMERICANA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 182

Norma E. Pfeiffer

(WITH PLATES VII–XI)

The family Burmanniaceae, chiefly tropical in distribution, is represented by about 50 species in Euburmanniae, 2 in Corsiae, and 18 in Thismiae. The geographical range of the first named group is by far the widest; its representatives are found in all tropical regions and extend into the temperate zone. In North America, they are found as far north as Florida, Alabama, and even Virginia. Corsiae are reported for New Guinea and Chile. Thismiae are represented by two monotypic genera, *Glaziocharis* and *Triscyphus*, recorded for Brazil, and by 15 species of *Thismia*, if zygomorphic forms are included.

Thismia is subdivided into four groups, *Euthismia*, *Geomitra*, *Bagnisia*, and *Afrothismia*. The *Geomitra* and *Bagnisia* divisions had been described as separate genera by earlier workers, but have recently been included in the genus *Thismia*. To date, the following species in this genus have been described in these regions:

Thismia Brunoniana Griffith (21), Tenasserim; T. Gardneriana J. Hooker (2), Ceylon; T. macahensis B. & H. (*Ophiomeris macahensis* Miers) (27), Rio de Janeiro; T. hyalina B. & H. (*Myostoma hyalina* Miers) (28), Organ Mts.; T. Aseroe (*T. Ophiuris*) Beccari (1), Borneo and Singapore; T. Neptunis Beccari (1), Sarawak; T. javanica J. J. Smith (9), Java; T. Winkleri Engler (7), Africa; T. crocea Ernst (*Bagnisia crocea* Becc.) (1), New Guinea; T. episcopalis F. Muell. (*Geomitra episcopalis* Becc.) (1), Borneo; T. clavigera F. Muell. (*Geomitra clavigera* Becc.) (1), Sarawak; T. clandestina Miq. (*Sarcosiphon clandestina* Blume) (12), Java; T. Rodwayi F. Muell. (29), Tasmania; T. Hillii (*Bagnisia Hillii* Cheesem.) (3), New Zealand; T. Versteegii J. J. Smith (12), Java.

Of these, the first 7 are of the *Euthismia* type, the eighth is the sole representative of *Afrothismia*, and the rest are of the *Bagnisia* or *Geomitra* group. The distribution of these is seen to be practically restricted to the Polynesian Malay region. In view of

this, the finding in the Chicago region of a form closely allied with these last is of decided interest.

Thismia (BAGNISIA) **americana,** nov. sp.—Herbae saprophyticae, tenerae, hyalinae, caulibus simplicibus erectis, radicibus elongatis glabris foliis bracteiformibus. Pedunculi uniflori, erecti vel curvati, 0.3–1 cm. longi. Flores subtiliter virides 0.8–1.5 cm. longi, circiter 6 mm. diametro. Perianthii tubus superus, obovoideo-oblongus, ore constrictus, lobis 6, quorum interiores tres apice conniventes, calyptram 3-stipitatam formantes; lobi alterni equales sed liberi. Stamina 6, fauci affixa, intra tubum deflexa filamentis brevissimis, connectivis maximis membranaceis in tubum deflexum connatis; antherae biloculares, loculis parvis distinctis parallelis, rima longitudinale dehiscentis. Ovarium breve, latum, 1-loculare, placentis 3 parietalibus, in cavo ovarii a pariete solutis. Stylus brevis, crassus, apice trifidus. Ovula numerosa, minuta, anatropa. Fructus turbinato-cupulatus, perianthii circumscisse deciduo truncatus, margine parum elevato cinctus. Semina numerosa, parva, oblonga, albuminosa; testa tenuis, hyalina, reticulata. Embryo parvissimus, in albumine inclusus.

Chicago, Ill., in open prairie, N. E. PFEIFFER.

The plant consists of a white root system, from which arise erect simple floral axes. The roots are about 1 mm. in diameter and vary greatly in length. The flowers are 0.8–1.5 cm. high, borne on an axis 0.3–1.0 cm. high. The perianth tube is conspicuously 6-nerved and with 6 minor nerves. The 3 petals, approximately equal in length to the 3 sepals, are connate at the apex. The mouth of the perianth tube is closed by a disk of tissue, with a central circular aperture surrounded by a raised ring. To this ring the 6 stamens are affixed, and are united into a tube which hangs downward inside the perianth tube. This stamen tube, largely made of the broadened connectives, bears the pollen sacs on the side toward the perianth wall.

The inferior ovary is one-celled, with three placentae which soon become free from the walls, appearing in a central plane as three free columns. The ovules are anatropous, numerous, and

small. There are two integuments. The seed contains a few-celled embryo imbedded in a mass of endosperm.

The entire plant is glabrous and white, save in the 6 divisions of the perianth, where free, and in the disk closing the perianth mouth. Here there is a delicate blue-green color, deeper in the raised ring about the aperture of the disk. Most of the plants have only this colored upper portion above the level of the soil, or of the surrounding moss, etc. The diameter of 5–6 mm. and a height above the soil of 4–6 mm. give an idea of the size of the flower. When the soil is carefully removed, the underground parts are found to be white and semi-transparent; they lie more or less parallel to the surface of the soil, at a depth of a few millimeters. There is no connection with other plants, although the roots of *Thismia* often lie in close juxtaposition with other roots. When the plant is so exposed (figs. 3 and 4), the flower plainly shows the typical THISMIAE structure; a tubular, 6-parted perianth, with the three inner members united at the apex. The leaves, as in other dependent Burmanniaceae, are reduced to white scalelike bracts, so closely appressed to the floral axis that they are readily overlooked.

The material was first discovered in August 1912, in a small space along the margin of a grass field. The habitat may be described as a low prairie, characterized by such plants as *Solidago serotina*, *S. tenuifolia*, *Rudbeckia hirta*, *Eupatorium perfoliatum*, *Asclepias incarnata*, *Iris versicolor*, *Acorus calamus*, and *Agrostis alba vulgata;* and on the soil itself *Selaginella apus*, *Aneura pinguis*, and *Hypnum*. Usually the *Thismia* grows in spots where the soil is not closely covered by *Aneura* and *Selaginella*, but it may be found occasionally among the moss (fig. 3). The little plant is evidently protected both against strong light and great transpiration; but its habitat is in striking contrast to that of most of the other species of *Thismia*, which are found in rich-loamed primeval forests, in regions of great rainfall.

The plants were watched for stages in development during August and the first half of September, to the time when some fruits were obtained. In the season of 1913, visits to the field were made weekly, with the result that flower buds were found on July 1, about a month earlier than the first observation of the previous season.

The indications were that the underground parts had wintered over, although seed-germination may have occurred and been overlooked, since the flower is all that appears above ground.

Earlier descriptions of the Burmanniaceae gave little attention to any but the gross features, which were in the main correctly interpreted. Until recently, the work in anatomy has been done largely by JOHOW (25, 26) in *Apteria setacea*, *Gymnosiphon refractus*, *G. trinitatis*, and *Dictyostegia orobanchioides*. The saprophytic forms worked with have scaly rhizomes, from which the flower stalks arise directly, as in *Thismia*. The adventitious roots are reported as being simple, with corky endodermis and a single, greatly reduced vascular bundle of lignified, dotted vessels, arranged in two concentric rings about one central spirally thickened element. The rhizome is described as having a structure much like that of the root. The erect stem or floral axis is credited with having bundles showing distinct xylem and phloem in most forms. The exceptions are *Apteria* and *Gymnosiphon trinitatis*, which have such small bundles that the differentiation is difficult to recognize, according to JOHOW. Nevertheless, he reports all cells of the bundle as lignified.

Recently ERNST and BERNARD (9–20) have added largely to the knowledge of the anatomy of different saprophytic forms. They have considered *Thismia javanica* J. J. Sm., *T. clandestina* Miq., *T. Versteegii* J. J. Sm., *Burmannia candida* Engl., *B. Championii*, Thw., and *B. coelestis* Don (*B. javanica* Bl.). In these forms, the vascular elements in the root are much reduced; in *T. javanica* (10) the bast alternates with thin-walled parenchyma cells about a central woody area, which is separated from the former by parenchyma cells. The xylem region is figured as consisting of as many as 13 vessels. The fungus occurs in these roots in a patchy arrangement, infecting one group of cortical cells and not another. In the uninfected cells starch is common.

In *T. clandestina* and *T. Versteegii* (13), a similar situation as regards arrangement of vascular elements is found, but the xylem is not so conspicuous in amount. In the former species, there is but one subepidermal layer of fungi, in the latter two, the outer of which is the coarser.

The xylem in *Burmannia candida* Engl. (**16**) is represented by but two spirally thickened cells in the central cylinder; occasionally there is only one, seldom three. In addition, there are parenchyma cells and phloem. *B. Championii* (**16**), in contrast to this, has a central cylinder largely made up of xylem elements, with no phloem evident. *B. coelestis* (**19**), a chlorophyll-containing form, shows a similar simple situation as to root anatomy.

In all the forms investigated, the floral axis has well developed collateral bundles. The vascular cylinder is sometimes surrounded by a ring of sclerenchyma tissue, as in *Burmannia candida* and *B. Championii*. The endodermis is usually distinct. Some of the cortical cells contain raphides. In *Burmannia candida* some of the surface cells are much like stomata in form, with pores always open. In *B. coelestis*, a chlorophyllous form, there are normal functioning stomata, in contrast to the usual lack in saprophytic forms.

In *Thismia americana*, superficial examination of the underground structures shows a relatively large number of buds in all stages of development. These occur not only on the main structure, which would appear to be a rhizome, but also on the structures which are very evidently roots appearing at the base of the floral axis. On examination of prepared sections, it appears that the histology of the main structure and of these secondary roots is identical, even to the appearance of a cap at the tip. Because of this fact, these structures, whether primary or secondary, will be referred to as roots. It would appear in field material that roots originally secondary might later appear primary by the dying away of a portion which thus severs the connection with the mother plant.

In the older part of a root of *Thismia*, there is evident a very conspicuous epidermis (figs. 7, 14). This consists of large cells, more or less protuberant, but not developed into hairs in any region. The epidermal cells, in contrast with the cortical cells below the surface, are hyaline. The layer of cells immediately below the epidermis is packed with the thick-walled, branching mycelium of a coarse fungus. In fresh material the mycelium

appears brown. The septate hyphae are usually oriented with the long axis of the root, so that the cross-section of a root shows numerous cut ends (fig. 14), and the longitudinal section a more or less parallel arrangement of the interweaving hyphae (fig. 7). Below this single layer is a region of a varying number of cortical cells containing much finer, thin-walled hyphae. In these deeper parts, masses of protoplasm are frequently evident which strongly suggest the sex organs of some of the Peronosporales. These undoubtedly correspond to the "vesicles" reported by JANSE (24) in *Thismia clandestina* (*T. javanica* J. J. Sm.), which he was inclined to believe asexually reproductive bodies. BRUCHMANN considered similar bodies in *Lycopodium annotinum* to be oospores of *Pythium*. In *Thismia* there are also bacteria, probably corresponding to JANSE'S "sporangioles" and "spherules." All these fungal parts are intracellular. A few cells outside of the endodermis are free from fungi. These contain raphides which are common throughout the plant body.

The endodermis consists of a single layer of heavy-walled cells, larger than their neighbors. It encircles a region, probably conducting, of which only a few central cells (3–5) are spirally thickened (figs. 5, 6, 19). They are not lignified, however, and the spiral markings are very fine. Near the point of origin of a floral axis, the number of thickened cells is increased and lignification occurs. These vessels may be seen to connect directly with the vascular elements of the floral axis. The cells adjacent to these spirally thickened vessels do not show the dotted condition that JOHOW reported in the Burmanniaceae considered by him. On the contrary, though they are somewhat elongated, they are nucleate and retain their cytoplasm. They are undoubtedly parenchyma cells, and so the situation is similar to that in *Thismia javanica* J. J. Sm. and other forms investigated by ERNST and BERNARD.

In the outer part of the conducting region are seen a varying number of points of small cells devoid of contents (fig. 6). The arrangement is similar to that reported in other forms by JOHOW and by ERNST and BERNARD. It suggests a radial arrangement, with these groups of cells probably reduced phloem strands without sieve plates.

The growing region resembles that in any root. In a few milli-
meters at the apex there is a meristematic region of actively
dividing cells. Then there is the region of elongation and differ-
entiation. The origin of the different layers would seem to con-
form to the general situation in monocotyledons, with distinct
initials in calyptrogen, dermatogen, plerome, and periblem. This
would be in contrast to the situation in *Thismia Versteegii*, where
ERNST and BERNARD report a common initial for epidermis and
root cap. In *Thismia americana* the tip region of the root is free
from fungi, but the tissue formed is rapidly invaded by the mycelium
from older parts. In no case was new mycelium seen to penetrate
the epidermis and so enter the uninfected region, as reported by
JANSE in *Thismia clandestina* (*T. javanica* J. J. Sm.).

Compared with that of the root, the anatomy of the floral axis
is complex (figs. 8–10). Here the vascular elements are arranged
in a cylinder of 3–6 bundles. In the early stages the number is
very apt to be 3; in the older axis, near the apex, there are divisions
of the original bundles, giving a larger number, frequently 6. More
may be seen where branches go from the original bundles.

Each bundle consists of definite xylem elements and a mass of
cells with slightly thickened walls (fig. 10). The xylem is slower
to appear than the latter, which are early clearly distinguishable
(fig. 8). In mature parts, the small clear cells appear in the same
relation to xylem as phloem usually does, but they show no sieve
plates so far as can be determined. Nevertheless, it seems probable
that these elongated cells function as phloem. The xylem vessels
have lignified and spirally thickened walls and their number varies
from 2 to 15 in each bundle. The large number, the conspicuous
spiral thickenings, and the lignification, as well as the greater and
more definite phloem development, are quite in contrast to the
condition found in the root.

A single strand of a few xylem vessels and phloem cells supplies
each of the bractlike leaves (fig. 11), which are very thin and rela-
tively broad. There are also branches of the main cylinder sup-
plying the floral parts and producing the conspicuous nervation of
the perianth.

There is no definite endodermis or pericycle in the floral axis,

nor is there a ring of sclerenchyma about the vascular cylinder as reported for some other burmanniaceous forms. As might be expected, no stomata were found; the corollary of no air spaces follows logically.

The floral axes appear to arise a short distance back of the tip of the root (figs. 4, 20). The first external evidence of their development is a single small excrescence (fig. 20a). Later two growing points, usually point upward, are distinguishable. Growth is quite rapid and soon results in a first root and a floral axis (fig. 20), from the base of which other roots take origin (figs. 21, 22).

In prepared material, the earliest stage in the development of the bud is shown in fig. 12. A region of rapidly dividing cells occurs below the epidermis in a somewhat arched mass. At this stage the main root itself is in such an undifferentiated condition that the endodermis and neighboring tissues are not yet distinct. In slightly older stages, a break is seen to occur between the cortical cells of the root and the growing cells of the endogenous branch, which now has a slightly lobed margin (fig. 13). At this time, the beginning of the first root to be developed may be seen (figs. 13, 19) as a mass of meristematic tissue to one side of the floral bud. By rapid growth the root overtakes the stem from which it originated, so that when the two structures have emerged a little beyond the boundary of the main root, they are about the same size (figs. 14, 15). At this time the floral part is still protected by the arch of primary root cortical tissue, but the root tip soon breaks through the cortex, becoming much the longer organ (fig. 16). A renewed growth of the floral axis and the development of other secondary roots from the main floral axis (fig. 17) finally result in a horizontal position of the first root, which had previously stood erect beside the floral axis.

In the development of the axis, the rudiments of the bract leaves appear laterally (fig. 17). After elongation and the development of the leaves, the differentiation of the floral parts occurs (fig. 18). The perianth tube develops early. At the same time, the stamens begin their development. The ovary with its ovules is late in appearance, a case similar to that in Orchidaceae. When

the ovules are first beginning to be evident, the microsporangial tissue is well defined.

There are, as usual, four microsporangia in early stages (fig. 23), which later fuse to form the two pollen sacs (fig. 28). The early stages show the stamens bent inward and downward, but not connected with each other. Later growth, particularly of the connectives, makes a continuous tube, which is, however, easily separated into the constituent stamens (fig. 28). This tube extends beyond the sporangia, which occur on the side toward the perianth wall. In mature stages the pollen grains are slightly oval. They are very pale, almost transparent, with a pale green cast, due to little bodies, probably fat, many of which also occur in the perianth parts. The microspores are loose and free, not massed together as in pollinia of orchids. Before shedding, the generative nucleus divides (fig. 29). A granular mass in the spore suggests the presence of a prothallial cell, but failure to secure stages in the present investigation must leave this doubtful at present.

The ovules, very many in number, develop on parietal placentae (fig. 24), which swing free from the ovary walls in the center (fig. 18). At this level ovules project on all sides of the placental column. In early stages the numerous primordia appear as in fig. 18. The fully developed ovule shows two integuments (figs. 26–27). It is anatropous, with a long funiculus. As JOHOW (26) and TREUB (30), and lately ERNST and BERNARD, reported, there is a conspicuous differentiation of a few of the nucellar cells at the base of the embryo sac. This seems to have no significance at present.

The seed is minute, with a testa two cells in thickness. The outer layer is composed of large, almost transparent cells. The inner one is constructed of smaller cells, with more contents, often appearing oil-like. The seed has a very evident endosperm, with cells of relatively large diameter, and an inconspicuous embryo of a few cells (fig. 30). In all respects it seems to agree with the accounts of TREUB (30) and JOHOW (25, 26), the former of whom first correctly interpreted the endosperm. MIERS, in 1866, declared that the seed of *Myostoma* contained no embryo. Later, GRIFFITH interpreted the entire content of the seed as embryo. TREUB,

in 1883, found a weakly developed embryo of 3 or 4 cells in a mass of endosperm in *Burmannia maburnia* and *B. javanica*. JOHOW, in 1885, reported a similar situation in *B. capitata* with a 10-celled embryo, and in *Apteria* one with 4 cells. In *Thismia javanica*, ERNST and BERNARD (11) have found a more strongly developed embryo with 4–6 tiers of cells. *Thismia clandestina* (14) has a still better differentiated embryo, with a 3-celled suspensor above a spherical body, the outer cells of which are differentiated from the inner. *T. Versteegii* (14), a closely related form, has on the other hand a simple embryo. *Thismia americana* then would seem, in its embryo situation, to resemble this last species and forms like *Burmannia javanica* and *B. maburnia*.

No case of polyembryony has been found, such as was reported by ERNST (8, 20) in *Burmannia coelestis* Don, a form developing embryos apogamously. Here the number of embryos was one, two, or three, dependent on whether the egg alone functioned, or the synergids were also active. In the earlier history ERNST found no reduction division to occur in the formation of "megaspores." Stages have not yet been obtained in *Thismia americana* to work out the sequence here, but assuredly, at maturity, only one embryo in each seed has so far been found.

The arrangement of parts in the flower seems such that insect pollination would be necessary, unless a situation similar to that in *Burmannia candida* Engl. and *B. Championii* existed. Here the pollen grains germinate in the sporangia, and the pollen tubes grow toward the style branches. No indication of this condition was found in *Thismia americana*.

Up to date, the few attempts at germinating the tiny seeds have been fruitless. It is to be hoped that a larger harvest may give a better opportunity for positive results. The relation of the fungus inhabitants to the developing plant might be better worked in this connection than with the mature plant. Since the fungi occur in the root, the absorptive region, and not in the stem, they would seem to have some connection with water and food supply. Microchemical tests show that in the root there is a very large supply of reserve food in the form of oils or fats. Contrary to the results of ERNST and JOHOW, no sugars or starch are present in

large enough amounts to detect by microchemical means. As indicated above, large amounts of calcium oxalate are present in the form of raphides throughout the parenchyma tissues of the plant body. This is probably to be related to the presence of the fungi.

The green oil-like bodies in the perianth parts gave in spectroscopic tests an absorption in the blue band. The coloring matter is not easily soluble in alcohol.

Further features in the morphology and cytology of this plant will be presented in a later paper.

Summary

1. The characters of *Thismia americana* are deemed sufficiently different from those of other members of the genus to warrant the description of a new species.

2. The main subterranean structure cannot be distinguished from a root, having a similar anatomical structure, including a root cap.

3. The root shows great reduction. The xylem is represented by 3–5 central spiral elements, the phloem by 4–6 small groups of cells. A radial arrangement is suggested in the grouping.

4. The vascular cylinder of the floral axis consists of 3–6 bundles, with xylem and phloem collaterally arranged. The xylem is composed of spiral lignified vessels. No sieve plates are distinguishable in the phloem.

5. The floral axis and first root arise from the main root endogenously. Other secondary roots arise from the base of the floral axis bud.

6. The ovary is slower in development than the other floral parts. Microsporangia are well developed when ovules first appear.

7. The ovules are anatropous, and have two integuments.

8. The embryo, consisting of a few cells, is imbedded in a mass of large-celled endosperm.

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EXPLANATION OF PLATES VII–XI

All figures, except 1, 2, 3, 4, 20, 21, 22, and 28, were drawn at the level of the table with the aid of a Spencer camera lucida under Spencer objectives 16, 4, or 1.8 mm., and oculars 2, 4, or 8. The following abbreviations are used: b, bud; br. bract; e, epidermis; fa, floral axis; ii, inner integument; oi, outer integument; lt, leaf trace; l, fungus infected layers; m, microsporangia; mr, main root; o, ovary; p, phloem; p', perianth; pw, perianth wall; rc, root cap; s, style; sr, secondary root; $s'r'$, second secondary root; x, xylem.

FIG. 1.—Side view of plant of *Thismia americana*, in situ; ×2.

FIG. 2.—View of flower from above; petals cut apart at apex and folded back; ×4.5.

FIG. 3.—View from above of group of flowers undisturbed in natural situation; the oldest flower appears at the right; ×4.5.

FIG. 4.—View from above of plants from which the soil has been removed; the white root portions are evident with their buds; ×2.6.

FIG. 5.—Longitudinal section of central cylinder of root; ×266.

FIG. 6.—Cross-section of central cylinder of root; ×266.
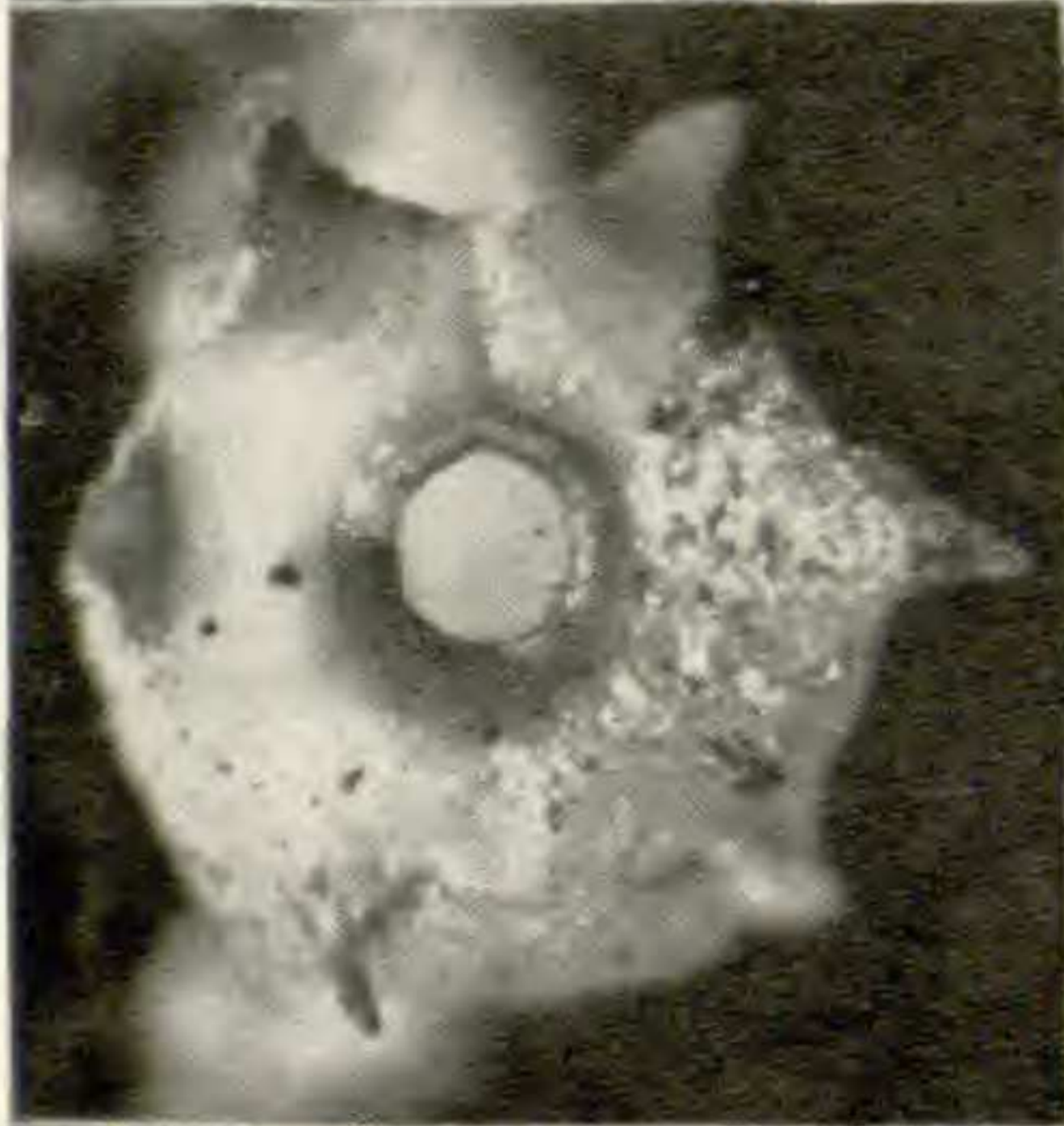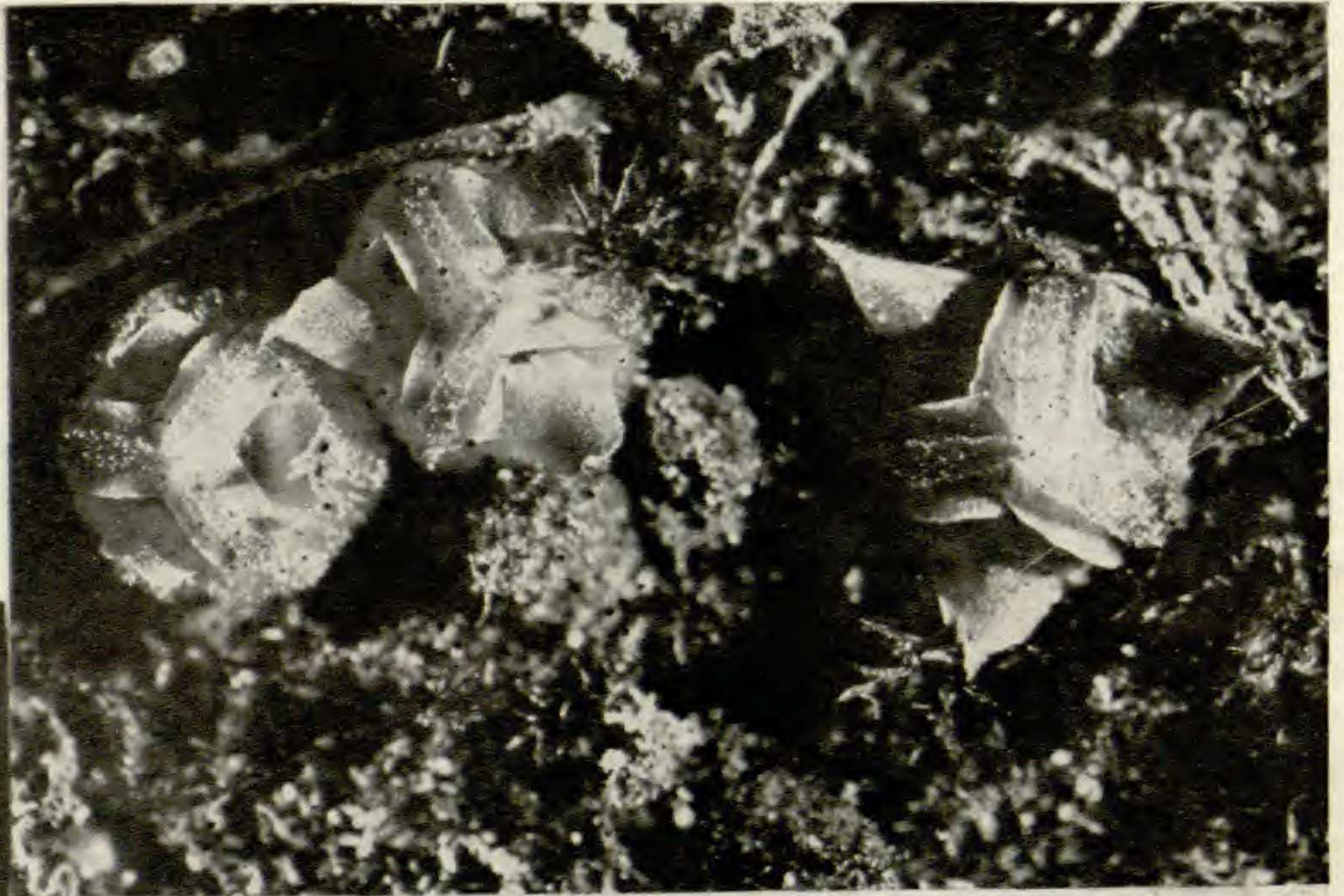
FIG. 7.—Portion of root in longitudinal section, showing subepidermal fungus infected layers, and epidermis free from fungi; ×266.

FIG. 8.—Cross-section of central region of young erect axis, showing early phloem development; ×266.

FIG. 9.—Diagrammatic cross-section of erect axis and bract leaves; the outlined portion of the axis proper is shown in fig. 10, of the leaf in fig. 11, with higher magnification; ×35.

FIG. 10.—Detailed drawing of portion of cross-section of floral axis; one leaf trace supplies the next leaf; ×266.

FIG. 11.—Detail of portion of cross-section of leaf, showing single, simple bundle; ×266.

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