583.821

Sm5s

A.C. Smith

Aphyllon uniflorum, Gray.

1891
1892
1893
1894
1895
1896
1897
1898
1899
19001891
1892
1893
1894
1895
1896
1897
1898
1899
1900

The Structure and Parasitism of *Aphyllon* *Uniflorum*, Gray.

(WITH PLATES XIII-XV.)

BY AMELIA C. SMITH, B.S.

Aphyllon uniflorum, or the Naked Broom-rape, belongs to the large parasitic order of the *Orobanchaceæ*, and is by some included in the genus *Orobanche*. It is typically a North American species, and is a pure parasite, being without chlorophyl. The present study was undertaken at the suggestion of Professor Macfarlane, and was carried out under his direction. All of my material has been collected from one very limited locality at Glenolden, Pennsylvania, where it grows luxuriantly. It appears toward the end of May, when Aster plants are about nine inches high, and by the end of June the seeds are matured and the plant is withering. I have invariably found it parasitic on the roots of *Aster corymbosum*. Chatin states that it is parasitic on *Solidago* and other Synanthæræ, while Beck gives the following list of host-plants: Species of *Artemisia*, species of *Solidago*, *Sedum stenopetalum* (!) By carefully cutting out and lifting a large sod containing several Asters and a clump of *Aphyllon*, and then washing away the soil until the roots were exposed, I was able to trace the root-connections with certainty.

METHODS.

Some of my material was killed in saturated aqueous solution of corrosive sublimate, a smaller quantity in absolute alcohol, and a great deal of it was simply preserved by placing it at once in 70 per cent alcohol. For general structure, all of the above methods gave equally good results. For

histological detail, and for embryological study, all of these methods proved equally bad. The protoplasm was somewhat shrunk even in the best specimens, and of course this was especially marked in the macrospore and surrounding cells of the ovule.

GENERAL MORPHOLOGY.

The plant is of a pale purplish-white color, and attains a height of from four to five inches. The roots are thick and fleshy, arise in clusters from the base of the stem and branch quite freely in all directions. Roots forming parasitic connections either end in a knob-like sucker, or (as is more usual) may continue past the sucker and end as a soil-root. Sometimes one *Aphyllon* root forms several suckers on the same or on different *Aster* roots. The soil-roots are more numerous than the parasitic ones, and from the structure of the former it seems probable that they are functionless as absorbing agents, and serve merely as hold-fasts.

The stem is short, fleshy, and relatively very thick, often more than one-quarter inch in diameter, and from one to one and a half inches in length. It may branch several times at the base, or may remain unbranched. Foliage leaves are entirely absent, or else are represented only by one or two very thin scale-leaves at the base. The bracts are the conspicuous leaves of the plant, and in a stout, vigorous specimen may number five to ten. In the axils of the upper bract-leaves are developed the long, hollow scapes, each bearing a single irregular, purplish-white flower. Upper bract-leaves, scape and flower are thickly clothed with glandular hairs.

I have found no trace of any perennating structure, and the plant seems to be strictly an annual.

STRUCTURE OF THE ROOTS.

The epidermis is of flattened, somewhat thick-walled cells. Some contain globules of a peculiar oil-like substance, but it

is not uniformly present, and some of the cortical cells show it also. I have found no trace of a symbiotic fungus in the epidermis.

Beneath the epidermis is the cortex, some ten or twelve cells deep. These cells contain many small, rounded starch grains, which are usually placed on the lower and inner sides of the cell. Chatin states that the epidermis contains fine granules, and the parenchyma large granules, "ni verts ni amylacés," but Koch states that starch is invariably present in the roots of *Orobanche*. Chatin may possibly have reference to the oil-like globules mentioned above.

Within the cortex is a reduced and degenerate bundle-system. The bundle-sheath is quite absent in some roots, in others it is represented in patches. The arrangement of wood and bast varies considerably. It is most commonly diarch. A modification of this is found, in which the wood projects on one side of the bundle, so that the phloem of that side is subdivided. A smaller proportion show a triarch arrangement, while in some there seems to be an indiscriminate distribution of wood elements. The xylem consists of rather short, pitted-reticulate elements, and though less in bulk than the phloem, is better differentiated. The phloem is composed of elongated elements, filled with highly granular contents, in which nuclei frequently persist. Sieve-tubes seem to be entirely absent. Protoplasmic connections between the cells corresponding functionally in all probability to similar processes in sieve-tubes were sometimes observed.

Root-hairs are either entirely absent, or are doubtfully represented by a few small, widely scattered, dermal papillæ. Absorption must therefore be impossible for these roots. This is in harmony with Koch's statement as to the total absence of root-hairs in *Orobanche speciosa*, *O. minor*, *O. ramosa*, and *O. Hederæ*, which he studied embryologically. Koch finds a root-cap on the soil-roots, *i. e.*, the secondary

roots of the above-mentioned species of *Orobanche*. They do not seem to be present in *Aphyllon*, but as I have not obtained any very young stages, it is possible that the root-caps are formed here also, and later slough off.

PARASITIC CONNECTIONS.

Parasitic connection with the host is effected by large haustoria, which fasten upon the host-root. The *Aster* roots are usually less than half the diameter of the *Aphyllon* root, but are harder and more woody. As a rule, they are not shriveled beyond the point of contact, but pass through the cluster of *Aphyllon* roots and enter the soil beyond them. The host-root is not completely surrounded by the sucker, but usually remains distinct and quite unmodified in structure on the side away from the parasite. The sucker is covered with an epidermal layer similar to that over ordinary *Aphyllon* roots, and this is quite continuous with the epidermis of the host-root. Beneath the epidermis the haustoria are composed of parenchymatous tissue, with strands of bundle-tissue, which branch almost at right angles from the bundle-tissue of the main root. This parenchyma spreads and mingles with the parenchyma of the host so intimately that it is impossible to distinguish their boundaries (Plate XIV, Fig. 2). The xylem and phloem elements of the parasite pass into the xylem and phloem regions of the host, and mingle with the corresponding elements of the host-bundle. The general position of the bundle of the host, is little modified however, and there seems to be no separation and isolation of bundle elements from the host-root within the tissue of the parasitic tubercle, such as occurs in *Conopholis*.¹

¹ L. L. W. Wilson, "Observations on *Conopholis Americana*," Bot. Contrib. Univ. Penn., vol. ii, p. 12.

STRUCTURE OF THE STEM.

In cross section the stem shows an epidermis of small flattened cells, thick-walled on the outer side (Plate XIV, Fig. 3). Beneath is the cortex, composed of large, rounded cells; there are usually from eight to ten layers of these cells, although the stems vary considerably in this respect. The cortical cells are closely packed with large rounded starch grains. Within is a more or less continuous ring of degenerate bundles, widely separated in some places by medullary rays. Within the bundle-ring again is the pith, its large rounded cells packed with starch grains.

The bundles are arranged in the usual manner, with external phloem and internal xylem. A reduced bundle-sheath is present as a frequently interrupted ring of small rounded cells. The phloem consists of elongated elements with granular contents, which are sometimes nucleated. As in the root, sieve-tubes seem to be entirely absent. The protoxylem consists of one or two spiral tracheæ with cells. The secondary xylem consists of short pitted-reticulate tracheæ, strongly indurated. A cambium is not generally present, although some stems show interrupted lines of small cells which may doubtfully be interpreted as cambium. Although the xylem elements are fairly numerous in root and stem, it seems probable that the wood has nothing to do with the conduction of nutritive liquids, but serves solely to support and strengthen the plant.

The presence of such quantities of starch in a colorless parasitic plant is somewhat perplexing. The starch cannot have been brought over from the host as such, since starch is insoluble, so that leucoplasts must be present, and in considerable numbers. They are, however, small and difficult to make out clearly. Moreover it is puzzling to see such an amount of reserve food stored in all parts of a purely annual

plant. Koch states that the large amount of starch stored up in a young plant immediately after germination, is to insure it against starvation in case the host perishes. But starch is present in great quantities when the seeds are nearly or quite ripe, and it is passed into the soil with decay of the plant. It can scarcely be wholly to insure a supply for the endosperm, for the amount stored there is infinitesimal compared to that in the entire plant. Further, the conditions of germination preclude the possibility that the starch is present in order that the seeds may find a rich nidus in the decaying parent plant.

BRACT-LEAVES.

The bract-leaves are thick at the base, gradually thin out at the top, and are closely appressed to the stem. The epidermal cells are small and flattened. The mesophyll is packed with starch, and is supported by a few strands of bundle-tissue, which enters the bract as one strand, and quickly subdivides. The tips of these leaves are very slightly trifid, a fact that perhaps points to a three-lobed ancestral leaf. The lower bract-leaves differ markedly from the upper. The lower ones have neither stomata nor hairs. The upper ones have numerous stomata on the free outer (morphologically under) surface, and the tips and outer surfaces are clothed with multicellular, capitate hairs. Between these two extremes, selecting a plant with five leaves, there are transitional stages.

THE FLOWER.

The flower is irregular, produces a five-parted calyx, a five-parted bilabiate corolla, four epipetalous stamens, and a superior bicarpellate ovary. Bracteoles are absent. The calyx is almost or quite regular. Its lobes are fleshy and bear hairs on the outer surface. The epidermis consists of irregular cells of wavy outline, and is pierced with many stomata. The

bundle-strands enter each lobe singly, but immediately divide into three main branches.

The upper lip of the tubular corolla consists of two somewhat recurved lobes, the lower of three lobes. Each lobe is supported by two main strands of bundle-tissue, which enter separately as branches of the bundle-ring in the floor of the flower. The outer surface of the corolla bears many hairs above the line where the calyx lies, against it, the inner surface not nearly so many. These hairs are all of the same type, having a stalk of several cells placed end to end, and a round head formed of (usually) eight radially arranged cells. The four epipetalous stamens are didynamous, the posterior pair being the shorter. The anther-lobes are formed in the usual way, having at first four and later two loculi. The microspores are small and spherical.

The unilocular ovary consists of antero-posterior carpels. Externally it is quadrangular in shape, corresponding to the positions of the four placentas, and the style bends forward so that the broad bilobed stigma lies at the anterior part of the mouth of the flower-tube. At the base of the anterior carpel is a large nectary sunk into the tissues of the carpel (Plate XV, Fig. 7). In cross section the ovary shows an epidermal layer of high columnar cells, the outer walls of which are thickened. Within are several (four or five) layers of rounded cells. The four parietal placentas are cushion-like ingrowths of similar rounded cells, the entire ovarian wall being packed with starch. A well-marked bundle-strand is present in the middle of each carpel, the position of the bundle being indicated externally by anterior and posterior grooves on the surface of the ovary. The small anatropous ovules are produced in great numbers (Plate XIV, Fig. 4).

The nectary shows in cross section seven to nine layers of gland cells, which are readily distinguishable by their small size, rounded outline, the absence of starch, their granular,

rather deeply-stained protoplasm, and large conspicuous nuclei. In the middle of the nectary, these cells extend quite to the bundle-ring, but on each side there is a rapid transition to the parenchyma of the carpellary walls. There is no special covering of epidermal cells over the nectary (Plate XV, Fig. 7). Externally, the gland appears as a small, rounded whitish swelling at the base of the ovary. The presence of this gland seems to have been overlooked by Chatin, for he characterizes the genus as one in which the ovary is unaccompanied by an hypogynous gland.

STRUCTURE AND DEVELOPMENT OF THE OVULE AND SEED.

The mature seed, which is very small and light, is surrounded by a tough, leathery coat, whose flattened cells have thickened indurated walls. The seed itself consists of a mass of endosperm cells, packed with starch, and enclosing a small primitive embryo whose cells contain little or no starch. The embryo is undifferentiated into plumule, cotyledons or radicle. These seeds will not germinate in water, nor in a nutrient solution made from the bruised roots of the host. Koch states absolutely that the seeds of *O. speciosa*, *O. ramosa*, *O. minor*, *O. Hederae* must come in contact with the host-root if they are to germinate, and Meehan finds the same for *Aphyllon*.

I have not yet worked out entirely the development of this seed from the young ovule, and between Figs. 2 and 3 (Plate XV), I have as yet no certain connecting links. Fig. 1 shows the first appearance of the macrospore-mother-cell in very young ovules. The ovule is here still orthotropous, and is a small conical upgrowth, covered with one layer of cubical cells and containing a large macrospore-mother-cell. Fig. 2, shows an older ovule. The ovule has here turned through an angle of nearly 90 degrees. The macrospore-mother-cell has greatly elongated, and is surrounded by

a clearly-marked nucellus, while the primine has grown nearly around the nucellus. Up to this stage there has been clearly no formation of tapetal cells, and (although my material was too badly shrunken to be very satisfactory) I have reason to doubt their formation at any time. I have observed many completely anatropous ovules, which contained within the three cell layers one much elongated, darkly-staining mass of protoplasm. Many of these showed two nuclei, but a clear unmistakable transverse wall could not be observed. Koch, in his "Entwicklungsgeschichte der Orobanchen," figures for *O. speciosa* the division of the macrospore-mother-cell into four, of which the upper one is the macrospore; and this division occurs when the ovule is turned half-way. If the macrospore-mother-cell does divide in *Aphyllon*, the divisions must occur at a much later period than they do in the related species described by Koch.

Plate XV, Fig. 3, shows a much older ovule. The integuments fully surround the nucellus, and the outer one is closely packed with starch, while the nucellus is pressed against by the structures within. Owing to the lack of closely preceding stages this ovule cannot be interpreted with complete certainty as yet. The probable interpretation, based upon the development of related plants, is as follows: The multicellular cell-body represents the mass of precociously developed endosperm, which has grown up around the egg-cell into a neck-like structure. The central cell is the egg, still unsegmented, and the long, plug-like body filling the apparent neck, is the suspensor, consisting of two cells. At the opposite end of the ovule, one cell represents the remnant of the antipodal cells, which have become shrunken. Such formation of precocious endosperm is common throughout the *Orobanchaceæ*, and in *Aphyllon* it seems to take place to a greater degree than in *O. speciosa*, as described by Koch, where the neck-like upgrowth of the endosperm around the suspensor is much less perfectly developed than in *Aphyllon*.

Plate XV, Fig. 4, shows the stage immediately following. The egg has divided longitudinally, and the suspensor consists of four cells. The lowest of these is destined to become the hypophysis of the future embryo.

In Fig. 5 the egg has divided into octants, and the hypophysis is plainly marked. The suspensor is still four-celled. The endosperm has increased greatly in bulk, and numerous small starch grains are found in its cells.

Fig. 6, of Plate XV, illustrates an almost mature seed. The integuments have become thin and flattened, and the endosperm contains much starch. The embryo has attained its full development. The regions are not clearly marked out, but the hypophysis here shows only anticlinal divisions. This is in harmony with Koch's statement that the primary root forms no root-cap.

SUMMARY.

1. *Aphyllon uniflorum* is parasitic on *Aster corymbosum*. The degeneration attendant upon its parasitic habit is expressed by :

- (a) Absence of chlorophyl.
- (b) Degeneration of bract-leaves.
- (c) Loss of root-hairs.
- (d) Reduction of the bundle-system, and the greater relative development of phloem than of xylem.
- (e) Small size of seed and primitive embryo, and the development of this embryo within a mass of precocious endosperm which completely surrounds the embryo and suspensor.

2. Parasitic roots form intimate connections with host-roots, but the host-roots are not entirely starved beyond the point of attachment.

3. Stomata are present on bract-leaves, flower-stalk, calyx and corolla.

4. A well-developed ovarian nectar-gland is present.
5. Starch is present in great quantities in roots, stems, leaves and carpellary tissue.

BIBLIOGRAPHY.

- Beck von Managetta, Monographie der Gattung *Orobanche*. (1890.) Bibl. Bot., Heft 19.
Baillon, Hist. des Plantes. (1891.)
Chatin, Anatomie Comparée des Végétaux, Plantes Parasites. (Paris, 1892.)
Gray, Asa, Flora of N. A.
Koch, Entwicklungsgeschichte der Orobanchen. (Heidelberg, 1887.)
Meehan, Thos., Proc. Acad. Nat. Sci., 1881. Part II. Pp. 160-162.
Wilson, Lucy L. W., Observations on *Conopholis Americana*. Contributions from Bot. Lab. of U. of P., Vol. II, p. 3.

EXPLANATION OF PLATES XIII, XIV AND XV.

- Plate XIII, Plant of *Aphyllon* growing on *Aster corymbosum*.
Plate XIV, Fig. 1. L. S. Root of *Aphyllon*.
Fig. 2. T. S. Root of *Aphyllon*, forming parasitic connection with root-tissues of *Aster*.
Fig. 3. T. S. Stem of *Aphyllon*.
Fig. 4. T. S. Ovary of *Aphyllon*, showing placental tissue with ovules.
Plate XV, Figs. 1, 2. Developing ovules of *Aphyllon*.
Fig. 3. Mature ovule, containing precocious endosperm and egg cell.
Figs. 4, 5. Upper part of endosperm surrounding segmenting egg cell.
Fig. 6. Macrospore enclosing endosperm and multicellular embryo.
Fig. 7. T. S. Nectary.

The Comparative Structure of the Flowers in *Polygala polygama* and *P. pauciflora*, with a Review of Cleistogamy.

(WITH PLATES XVI-XVII.)

BY CHARLES HUGH SHAW, PH. D.,

Professor of Botany in Temple College.

[Submitted to the University of Pennsylvania in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy.]

In the genus *Polygala* only two species, so far as known, exhibit cleistogamy. Both are natives of the Eastern United States. One is *P. polygama*, often abundant along our sandy coasts, the other is *P. paucifolia*, the beautiful so-called Flowering Wintergreen of more interior districts.

The former, alike from the abundance of the cleistogamic flowers it produces, and the presence of intermediate types now for the first time described, has been the chief subject of the present study and will be first dealt with.

The detailed description of the various types of flower may best be prefaced by recapitulating what is known of the flowers of the genus.

Conspicuous blooms are borne by all members of the genus. These are generally in racemose clusters, and are sometimes very showy. The typical aërial flower is very irregular. In the calyx the two lateral, interior sepals are greatly developed as petaloid wings. The corolla consists of three petals, one anterior and two posterior, the two lateral of the theoretical five being suppressed. Of the three the anterior one is greatly developed as a hood covering the stamens and pistil. The stamens are eight in number, the anterior and posterior ones of the theoretical ten being wanting. They are monadelphous, being united below, and

SMITH ON APHYLLON.

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

SMITH ON APHYLLON.

Fig. 1.

Fig. 7.

Fig. 2.

Fig. 4.

Fig. 5.

Fig. 3.

Fig. 6.

THE
LIBRARY
OF THE
MUSEUM OF
ART AND HISTORY
OF THE
CITY OF
NEW YORK

Gaylord Bros,
Makers
Syracuse, N. Y.
PAT. JAN. 21, 1908

UNIVERSITY OF ILLINOIS-URBANA

583.821SM5S

C001

THE STRUCTURE AND PARASITISM OF APHYLLON

3 0112 009970127