Obolaria virginica L.: A Morphological and Anatomical Study.

BY

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With Plate XIX and Woodcut 6.

FEW plants, as regards both habit and relationship, have puzzled botanists more than the one known as *Obolaria virginica*, and a comparison of the various diagnoses which have been made of it, even up to a recent date, shows that it is as yet generally very imperfectly known. To thoroughly understand this plant it is necessary to study it in a living state on the very spot where it grows. The many and diverse opinions expressed in regard to its true nature arise from a study of the dried material only.

The name itself has quite a history. The plant which is now dedicated to Linnaeus as *Linnaea borealis* was the first one to be called *Obolaria*, this name being applied to it by Siegesbeck. Gronovius, or rather Linnaeus himself, however, changed the name of this plant to *Linnaea borealis*, and transferred to our North American gentianaceous plant Siegesbeck's name, *Obolaria*, which it still bears. The history of this plant, however, is much older than its present name, extending back to the days of Plukenet and Morison. The former called it *Orobanche virginiana*, and in Morison's and Ray's works it is known under the same name. Later it was described by Clayton, but under no special name, it being

spoken of as *Anonymos humilis*, and it was after this that Linnaeus gave it the name it now bears.

The *Schultzia obolarioides* of Rafinesque does not seem to be identical with this plant, judging from a comment in the author's diagnosis, in which he says, 'It is very near akin to *Obolaria*'; and also from the fact that, according to his description, the calyx and corolla do not correspond with these organs in our plant. Notwithstanding these differences, however, Otto Kunze adopted the name given by Rafinesque, changing *obolarioides* to *virginica*, O. K.

Considered from a systematic standpoint, there is a great difference of opinion in regard to the classification of this plant. For instance, Elliott, Persoon, and Walter placed it under Didynamia, and Meisner under Scrophularineae; Endlicher believed it to be related to these families; Bartling, Clayton, Don, Jussieu, Lindley, Morison, Plukenet, Rafinesque, and Ray placed it under Orobancheae, while Linnaeus and Willdenow alone considered it as *Orobancheis affinis*. Credit is due to Nuttall for classifying it under the Gentianeae, and to Darlington for having observed that the stamens are equal and not didynamous.

Although the true systematic position of the plant has been ascertained, there still remain several points to be settled. The peculiar aspect of the plant, especially when dried, has led botanists to suspect that it is a saprophyte or even a parasite. Gray speaks of it as 'suspected as partially parasitic'; Johow says it is 'an almost chlorophyll-free humus plant'; Knoblauch believes it to be 'an imperfect saprophyte'; Gilg thinks it is 'doubtless a saprophyte'; and Don has declared that it is 'terrestrial, not parasitic.'

These statements, together with the diversity of opinion in regard to the supposed relationship to the Orobancheae, as indicated above, show the general lack of knowledge in regard to the true nature of the plant.

Notwithstanding the fact that elaborate studies of the *Obolaria virginica* have been published by Baillon, Gilg, Gray, and Knoblauch, there is as yet no detailed description

extant, and it is with the hope of adding to the knowledge of this plant and of encouraging botanists to find additional facts in regard to it that we venture to give here some data concerning it.

Various descriptions of the inflorescence of *Obolaria virginica* have been given. Gray first described it as centrifugal, but later described it as a raceme, with the flowers 'in clusters of three, terminal and axillary or solitary'; Bentham and Hooker considered it a spike. However, the fact is that the flowers are arranged in three, or, by abortion, one-flowered cymes. Often small specimens show only a single flower, which is terminal, and at the sides of which rudiments of two lateral flowers are usually found. In large specimens the number of normally developed flowers may reach twenty-one, with rudiments of twelve others, thus corresponding to one terminal and ten lateral three-flowered, or, by abortion, one-flowered cymes. This is a cymose inflorescence, which, according to Eichler, is common in the Gentianeae.

Usually the flowers are sessile, and the peduncles of the inflorescence short, excepting in the case of the lower ones. On examining the flowers two free calyx-leaves will be seen, and this singular fact has given rise to the supposition that *Obolaria* has no calyx, but two bracts instead. Linnaeus considered them a pair of bracts, while Elliott stated that they probably perform the function of a calyx. Even Baillon in his monograph of the Gentianeae described the flowers of *Obolaria* as 'flores asepali.' It is true that the calyx of *Obolaria* is very different from that of the ordinary Gentianeae, not only on account of the suppression of the two leaves, but also because those which are developed are, with the exception that they are smaller, similar to the stem-leaves and the bracts, having the same spatulate shape, with rounded apex, and exactly the same nervation. Their lateral margins are slightly involute, forming an envelope around the flowers, thus performing the true function of an ordinary calyx. Owing to the fact that the position of the calyx-leaves in the one-flowered inflorescence corresponds to that of true prophylla, being situated

In regard to the corolla, it may be said that this is regular, campanulate, and deeply four-lobed, as described by the various authors. In some specimens, however, we have noticed a five-lobed corolla. Notwithstanding this, these flowers had only two calyx-leaves, and the corolla was distinctly bilabiate, with the lower lip three-lobed. In such flowers there were but four normally developed stamens, with a rudiment of a fifth, corresponding to the supernumerary fifth corolla-lobe. The fact that some botanists have been led to believe that the plant is Orobanchaceous may be due to their having observed these abnormal flowers, and also from the singular foliage in connexion with the coralloid root-system.

Another point of interest which so far seems to have been overlooked, is that the corolla of *Obolaria* bears nectaries. When the corolla-tube of a living specimen is opened, there is distinctly visible at the base of each stamen, almost midway between the base of the filament and the base of the corolla-tube, a small, lobate, papilliferous scale (Plate XIX, Fig. 1). As this scale was found in all the flowers we have so far examined, it doubtless is a constant character.

Gilg has given a number of figures illustrating the nectary in the genus *Sweertia*. There is a great similarity between the nectary of *S. multicaulis*, Don, and that of *Obolaria virginica*, and therefore Gray is wrong in saying that the corolla of *Obolaria* has no appendages. Baillon's statement, 'les fossettes disparaissent dans les Bartonias et les Obolarias,' is, on the other hand, nearly correct, since the grooves in the corolla of *Obolaria* are very imperfect. Bentham and Hooker have placed our plant among the *Sweertieae*, with 'corolla efoveolata'; Gilg has separated our genus from the *Sweertieae* and their relations; and Knoblauch has followed Bentham and Hooker. The indications are, however, that *Obolaria* is closely related to the genus *Sweertia*.

Another fact which has not been previously noticed is that glandular hairs (Pl. XIX, Fig. 6) are present in the sinuses of the corolla. Baillon speaks of the presence of such hairs in the axils of the bracteoles (calyx-leaves), and Knoblauch

observed the same not only in the axils of the calyx-leaves, but also in those of the bracts and stem-leaves.

In *Obolaria* the stamens are equal in length. The anthers were figured by Gray as sagittate, but they are not strictly so; and the pollen-grains, which he described as 'globose and very smooth,' are oblong, with the exine distinctly granulate. The ovary is one-celled, and contains a large number of ovules, which are scattered all over the interior surface of the two carpels. In this respect it differs from the other Gentianaceae, with the exception of *Bartonia* and *Pleurogyne*; and as this last-named genus belongs to the Sweertieae, this is another indication that our plant is related to this group. The ovules are anatropous and monochlamydeous, and the funiculus is rather long. Occasionally, however, we have observed that some rudimentary ovules were atropous, and seemed destitute of any integument, thus resembling those of the genus *Voyria*.

The foliage shows a marked uniformity as regards shape and structure. The leaves are opposite, excepting those at the base of the stem, which are sometimes alternate. This, however, is usually due to an occasionally forced curvature of the stem while protruding from the soil. The shape of the leaves is spatulate, this form predominating in the stem-leaves, the bracts, and even in the calyx-leaves. At the base of the stem they are sometimes more or less scale-like. The position of the leaves is somewhat singular, standing in a vertical position and being often closely appressed to the stem and flowers, in which latter respect this plant shows a certain resemblance to the Orobanchaeae. The colour of the leaves is also characteristic, being of a deep purple hue, with only a slight shade of green. As we have before stated, several writers have expressed the idea that *Obolaria* may be partly or entirely destitute of chlorophyll. The colouration is due to the large amount of anthocyan dissolved in the cell-sap of the epidermis and present in the greater part of that tissue. In this way the chlorophyll is almost entirely concealed, since only the mesophyll is chlorophyll-bearing. By immersing the leaves in strong

alcohol, the anthocyan loses its colour, while the chlorophyll stains the alcohol a rich green. It may be added incidentally that it was by this same method that chlorophyll was discovered in the brownish-coloured *Neottia*, which for a long time was believed to be without chlorophyll.

The anatomy of the leaf also shows some points of interest. The cuticula is rather thick and wrinkled, and the cell-walls of the epidermis are strongly undulate, except where the strata cover the nerves, at which points they are almost straight. Stomata are present on both faces of the leaf, but are most numerous on the inferior face. Each stoma is surrounded by four or five cells, and is generally parallel with the longitudinal axis of the leaf (Pl. XIX, Fig. 2). We have observed, however, that some of the stomata, especially in the neighbourhood of the nerves, showed a somewhat different direction, this being due to the stretching of the surrounding cells (Pl. XIX, Figs. 3 and 4).

A fact worthy of notice is that the epidermis is but slightly coherent with the parts subjacent, this being observed not only in the leaves, but also in the stem and, in a very marked degree, in the ovary. An examination of the mesophyll shows that it contains the chlorophyll equally distributed in the various layers. A transverse section (Pl. XIX, Fig. 5) shows that the mesophyll consists of about seven layers of roundish cells; and, strange to say, this tissue does not show any differentiation into a palisade or pneumatic tissue. The leaf thus becomes isolateral. Although the isolateral leaves usually have a palisade-tissue developed on both faces of the leaf-blade, a few plants are known in which this tissue is entirely absent. This has, for instance, been recorded by Heinricher as characteristic of the parasitic genus *Thesium*, and it is somewhat surprising to observe a corresponding structure in our genus *Obolaria*.

The absence of palisade-tissue in *Thesium* has been explained by Heinricher as evidently depending upon its parasitic nature, but this explanation does not seem tenable regarding *Obolaria*. A careful examination of the chloro-

phyll in the leaves shows that it is able to provide its own starch, and this fact seems sufficient to prove that our genus is neither parasitic nor saprophytic. It is also true that the root-system, as will be shown later, does not show any parasitic connexion with the plants which grow in those places where *Obolaria* is generally found.

Concerning the mestome-bundles of the leaves, these are rather weakly developed, and contain only a very small group of leptome and a somewhat larger group of hadrome. Stereomatic tissue was found to be entirely absent, so that altogether the leaf shows a very simple structure.

The stem of *Obolaria* is quadrangular, very pale, and often curved toward the apex. The epidermis consists of rectangular cells, with very thin, straight walls (Pl. XIX, Fig. 7), covered with wrinkled cuticula. Stomata are present (Fig. 8), but they are very scarce. Only a small number of the epidermal cells contain anthocyan. The bark-parenchyma occupies the greater part of the stem-cylinder, and is composed of very thin-walled, loosely-connected cells, with very little chlorophyll and no deposits of starch. No stereome has been observed. Inside the bark-parenchyma is an endodermis (Pl. XIX, Fig. 10); this consists of thin-walled cells, which show the spots named after Caspary, and forms a closed sheath around the mestome-bundles, of which latter the hadrome-element forms the most prominent part. The leptome is developed, not only on the exterior face of the hadrome (Pl. XIX, Figs. 10 and 11), but also on the interior face, toward the pith, and we have in this way what De Bary has designated as 'bicollateral mestome-bundles.' Mestome-bundles of this form have been observed in numerous families, and have been described by various authors, for instance, Moebius and Petersen. According to Gilg, they seem especially characteristic of the Gentianoideae. The exterior leptome is well developed, and forms an uninterrupted ring around the hadrome-cylinder. The interior leptome, on the contrary, forms merely small groups, which border on the inner part of the hadrome. These groups are

generally scattered, but a few are connected with each other. It is not unusual, however, to observe some groups of leptome imbedded in the pith (Fig. 12), thus being separated from the hadrome. These isolated leptome-groups are very small, and contain only a few narrow, thin-walled cells. The hadrome is, as stated above, very strongly developed, and the tracheids are so thick-walled and tough that it is difficult to make good sections of the stem so as to get the pith and inner leptome well preserved for study. The pith is composed of thin-walled cells and occupies the entire inner part of the stem.

The root-system has several peculiarities. It consists of a relatively small number of fleshy, irregularly thickened, and wrinkled roots, which show only a few ramifications and are of a light brownish colour. The term 'coralloid,' as used by Morison, for these roots is, therefore, very well chosen. The roots are almost equally developed, there being no main root. In this respect our plant agrees with the Saprophytes, except the European species of *Monotropa*, in which a main root is developed. In our examination of the anatomical structure of the root we were surprised to find that root-hairs are entirely absent. A few of the epidermal cells had become elongated into short papilli, a fact that again reminds us of the Saprophytes.

An examination of a transverse section of a young root (Pl. XIX, Fig. 13) will reveal a thin-walled epidermis; a hypoderm of only one stratum; a broad bark-parenchyma; and a thin-walled endodermis, inside of which a pericambium surrounds the mestome-bundles. Two groups of leptome, separated from each other by a line of vessels corresponding to two separate groups, will also be seen, showing that the root is of the diarchic type. At this stage the root shows a normal development except that it lacks root-hairs. If an older, full-grown root (Fig. 14) is examined, it will be found to present a very different aspect. While the structure of the epidermis and the hypoderm agree with that of the young root, the bark-parenchyma will show a great increase

in regard to the number of strata and the size of the cells; moreover, the greater part of the bark-cells will be found to be filled with glomerules of fungal hyphae, showing that the root has become a mycorrhiza. This form of root was first described by Frank, and, so far, has been found only in a few Gentianaceae, viz. the saprophytic genera *Voyria* and *Voyriella*. According to Warming, mycorrhizae are characteristic of several Ericaceae and Orchidaceae which thrive only in a rich humus. In these, as in *Obolaria*, the mycelium is found exclusively in the bark-parenchyma. The mycorrhizae also occur in many trees, and Sarauw has given a monographic study of them.

In *Obolaria* the swelling of the roots is due to the presence of these fungal hyphae, which undoubtedly cause a certain irritation, not only of the bark, but also of the tissues inside of the bark. The cells of the endodermis (Figs. 15 and 16) show numerous divisions, both tangential and radial. The pericambium shows similar divisions and forms several strata, while the inner mass of the root-cylinder, the hadrome and leptome, undergoes a considerable disturbance as regards the arrangement of its tissues. The groups of leptome are imbedded in a huge mass of cambial layers, which surround a number of vessels, constituting the innermost part of the root-cylinder. As regards the arrangement of tissues, there is in this a marked difference from that observed in the young roots, as described above.

In the old root there is nothing to indicate its originally diarchic type. The interior tissues, from the bark to the hadrome, undergo an increase so sudden and irregular that the position of the various elements is changed and an abnormal development of cambial tissue takes place. This is all the more peculiar when it is remembered that our plant is annual. Had the anatomical structure of the root been known, there would have been good reason to suspect *Obolaria* to be saprophytic; but as the roots do not show any haustoria there was no reason to suppose it to be a parasite.

In discussing the question as to whether our plant is really

saprophytic, as has been supposed, it might be well to cite the principal features which characterize our genus. These may be divided into two categories: (1) Such characters as it has in common with the autophytic Gentianaceae, and (2) the characters by which it is related to the saprophytic members of the Gentianeae family. In the first category are the following characters: (1) The shape of the aerial leaves is spatulate, not scale-like; (2) the presence of chlorophyll in great abundance; (3) the presence of stomata; (4) the ability to produce starch; (5) the strong development of the hadrome in the stem; (6) the anatropous, monochlamydeous ovules. In the second category, comprising the saprophytic characters, are (1) the vertical, appressed leaves; (2) the non-differentiation of the mesophyll; (3) the imperfect root-system, that is, lack of root-hairs, few ramifications, and non-development of the primary root; (4) the root is a mycorrhiza; (5) the occurrence of some rudimentary ovules, these being atropous and destitute of integuments.

According to this characterization, it cannot be denied that our plant shows a singular position between the Autophytes on the one hand and the Saprophytes on the other. The structure of the roots would be rather abnormal to an autophyte, as would be the chlorophyll and the strongly developed hadrome to a saprophyte. In considering the characters of the saprophytic Gentianaceae, so admirably described by Johow, the following differences will be noted:—The saprophytic Gentianaceae have no chlorophyll, no stomata, and no lignified tissues, while all these are found in *Obolaria*. The only features, and these are unimportant, which *Obolaria* has in common with its saprophytic relatives are the non-development of the primary root, lack of root-hairs, and the lack of stereome. It grows in soil poor in humus, and in localities which are neither shaded nor very moist, conditions which do not seem especially favourable to Saprophytes. The saprophytic Gentianeae are all inhabitants of moist and shaded places, being found generally among decayed leaves or on the trunks of dead trees. Being one

of our earliest bloomers, its flowers are developed some time before the foliage of the surrounding trees and shrubs unfold, thus being fully exposed to the sunlight, against which it is protected by its waxy cuticula and the large amount of anthocyan contained in the leaves.

The absence of root-hairs in *Obolaria* is of course somewhat surprising in connexion with the non-development of the primary root. On the other hand, however, there are truly saprophytic Orchideae, that is, *Corallorhiza* and *Epipogon*, which have organs that perform the same function as root-hairs, and the European species of the saprophytic genus *Monotropa* possesses a primary root.

On account of the many intergradations between the Autophytes and the Saprophytes, it is almost impossible to draw any general distinctions. In regard to the Gentianaceae, most of which are Autophytes, it may be said that the genus *Obolaria* is a connecting link between the autophytic and the saprophytic genera; and although it has several characters in common with the Saprophytes, we are inclined to consider our plant an autophyte.

In regard to its systematic position, it is, as above stated, closely related to *Sweetia* and *Pleurogyne*: to the first by the presence of nectaries, and to the latter by the position of the ovules on the entire inner surface of the carpels.

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EXPLANATION OF FIGURES IN PLATE XIX.

Illustrating Mr. Holm's paper on *Obolaria virginica*.

(The letters in the Figures indicate as follows: *B*, Bark-parenchyma; *Ca*, Cambium; *End*, Endodermis; *Ep*, Epidermis; *H*, Hadrome; *Hyp*, Hypoderm; *L*, Leptome; *M*, Mesophyll; *P*, Pith; *P. H*, Protohadrome; *Pr*, Pericambium; *V*, Vessels.)

Fig. 1. One of the papilliferous scales from the corolla. $\times 65$.

Fig. 2. Stoma from the superior face of a stem-leaf. $\times 440$.

Figs. 3 and 4. Two stomata from the inferior face of a stem-leaf; these were taken from that part of the epidermis which covers the veins. $\times 440$.

Fig. 5. Transverse section of a stem-leaf. Some of the epidermal cells contain anthocyan (drawn with dots in the Figure), and the mesophyll forms a uniform tissue without being differentiated into any special palisade or pneumatic tissue. $\times 440$.

Fig. 6. Glandular hair from the axil of one of the stem-leaves. $\times 440$.

Fig. 7. Epidermis of the stem. $\times 440$.

Fig. 8. Stoma from the stem. $\times 440$.

Figs. 9, 10 and 11. Transverse sections of the stem, showing the epidermis and a part of the bark (Fig. 9), the endodermis, a group of leptome, a part of the hadrome (Fig. 10), two groups of the inner leptome, and a part of the pith (Fig. 11). $\times 440$.

Fig. 12. A very small group of the inner leptome imbedded in the pith. $\times 440$.

Fig. 13. Transverse section of a young root, showing a part of the inner layers of the bark, the endodermis, the pericambium, the leptome and hadrome. $\times 440$.

Fig. 14. Transverse section of a full-grown root, showing the inner layers of the bark-parenchyma, of which two cells show glomerules of fungus-hyphae. The endodermis and the pericambium show numerous tangential and radial divisions. Between the leptome and hadrome is a great mass of cambial tissue. $\times 440$.

Figs. 15 and 16. Two cells of the endodermis of a full-grown root showing radial and tangential divisions. $\times 440$.

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