NOTES ON HYDROCOTYLE AMERICANA L.

BY THEODOR HOLM.

(With Plates xlvi, xlvii.)

INTRODUCTION.

It is the intention to present, under the title "Notes," a series of contributions to the life-history of some North American plants; their manner of growth, illustrated by morphological representations of the differences in the development of their rhizomes, stems, etc.; their germination, and, finally, remarks upon their anatomical structure. But it is to be remarked that it would be difficult to give notes of this kind in anything like a systematic order, since the observations are usually made incidentally and at different seasons of the year. I hope, however, to be able to give these notes in such a manner as to give a more or less complete idea of some of our more interesting plants, whose development and structure has either not been described or is only briefly alluded to in the systematic works.

There are many circumstances in the life-history of our plants which are imperfectly known, and, although they may seem to be of little interest, they nevertheless have a certain value for the complete understanding of the organization of the plants, and therefore I do not hesitate to publish these observations under the title "Notes." Furthermore, the differences in the development of the organs may often show several good characters, which ought to be given in the diagnosis of the plants, especially when they admit the distinguishing of otherwise nearly allied species.

Purely systematic studies have furnished many excellent contributions to the knowledge of our flora; the distribution of plants, their different stations, their liability to variation, etc.; but it seems more than probable that had botanists given more attention to observations of this kind, and especially to the germination of the plants, a subject that has been much neglected, we should have a better knowledge of the complete life history of our plants, and the systematic studies would at the same time be rendered valuable assistance.

HYDROCOTYLE AMERICANA L.

During a collecting trip this fall in the woods along the Eastern Branch of the Potomac, Prof. Lester F. Ward, who has kindly shown me the most interesting localities in the vicinity of Washington, called my attention to Hydrocotyle Americana, which we found growing in
a moist, shaded place, and which, he informed me, he had collected several years ago, observing at the time some peculiar organs, apparently small tubers, which evidently belonged to the plant. He was unable to find descriptions of these organs in the systematic works, and as he was unable to undertake their examination himself he requested me to investigate them. The plants, on being carefully dug up, showed a number of tubers, hanging by whitish stolons from the axils of the lower leaves. I examined them, and found that the organs were true tubers, each consisting of several nodes, and that they must undoubtedly be of considerable importance for the propagation of the plant.

In presenting the results of this examination, I shall first make some remarks upon the diagnosis of our plant by the different authors who have described it. The presence of the tubers has been mentioned recently by Dr. George Vasey,* who observed them in 1833 and published a short note upon them, in which, however, he only mentions their presence. He says: "I was surprised to see a number of whitish threads hanging from the axils of the lower leaves. I found that near the extremity of these was a short oblong or cylindrical tuber, and these tubers were undoubtedly for the propagation of the plants." Dr. Vasey also sent the plants to Dr. Asa Gray, who replied that he had often observed the "threads," but never the tubers.

It seemed somewhat singular that this plant, one of our more common species, should never have been more carefully examined before and the presence of these tubers detected, and I determined to look at the descriptions of it in the systematic works. In Gray’s Manual of Botany, 1870, the plant is described as having the "stems filiform, branching, spreading, and creeping," but the author says nothing in regard to its subterranean organs, either of the root or of the presence of any rhizome, and I found the same to be the case in some other systematic works of a more recent date. On turning to the older authors, curiously enough it is found that the fact of our plant being "tuberiferous" was mentioned more than eighty years ago by a French author, and in such a manner that it can not be doubted that he had examined the plant and found at least one tuber. This author is A. Michaux, who in his Flora Boreali Americana, published in the year 1803, has written in his diagnosis of Hydrocotyle Americana, "Radice tuberosa," and, as will be shown later, even if his expression "radice" may not be correct, he was evidently a careful observer, and is probably the first author who mentioned the circumstance.

On further examining the literature, of which unfortunately only a small part is accessible to me, I found that a few years after Michaux, Fr. Pursh† had described the plant as being "Herba glabra, tuberosa." It was supposed that the plant would be very exactly described by

†Flora Americ. septentr., Vol. 1, 1816, p. 190.
Achille Richard in his Monographie du genre Hydrocotyle;* but he says only: "Elle (H. Americana) a, selon Michaux, une racine tubéreuse."

Of all the species mentioned in De Candolle's Prodromus† only Hydrocotyle interrupta Muhl. was described as being tuberous, namely its variety tuberosa: "Caule hinc inde ad nodos tumido et tuberoso," which tuberosity then is quite different from that of H. Americana, and nothing has been written about the tubers of our plant. Eaton‡ is another American author who has mentioned it as "tuberous," but from his observation in 1833 until 1886 the plant does not seem to have been observed as being "tuberosa" nor "tuberiferous."

The stolons, Vasey's "tuberiferous threads," seem to have been known before, for Torrey§ has described the plant in this manner: "Stems with long suckers." It has also been mentioned by Darlington|| as having "Filiform runners from the axils of the leaves," and further by Chapman,¶ who has called the stem "stoloniferous;" but these remarks are all that we know about them, and it is not perfectly sure that these authors have intended to describe the true stolons, since they may have seen only the runners of the plant.

On turning to the specimens of Hydrocotyle Americana, it is first to be remarked that the plants, which I have had the opportunity of examining from the Eastern Branch, and others from different places preserved in the herbaria of the U.S. National Museum and of the Department of Agriculture, all the complete individuals show that they have been developed from tubers. The development from the seed is not known, but it is to be supposed that there is little difference between this and the other method, excepting that it would be interesting to know whether the primary root has a tendency to be tuberous. There is no doubt that the plant is able to propagate itself by seeds, for many of the specimens I have seen bore fruits which were all normally developed. Plate XLVI, Fig. 1, illustrates the lower part of the stem of Hydrocotyle Americana, and shows the tuber from which the plant has been developed. We see that the rhizome consists of the tuber and a single internode, bearing a scale-like leaf, from the axil of which a long stolon has been developed; we see further that another branched stolon has been developed from the axil of the lowest complete but now faded leaf of the stem. From the axils of the other leaves at the upper part of the stem we see (Plate XLVI, Fig. 2) that two runners have been developed, and at the summit of the stem we find the inflorescence, which is not figured, since it is already well known.

It will be observed that our plant has two kinds of vegetative propagation: by stolons, ending with tubers, and by runners. Now, it

*Ann. sc. phys., IV, Tab. 55, Fig. 10, 1820.
†A. P. De Candolle: Prodromus syst. nat. regni vegetab., IV, 1830.
must be remarked that the stolons are always to be found under ground, but usually near its surface, and the runners are creeping on the earth. But it is probably a mere matter of accident as to whether these organs of propagation are developed as stolons or as runners. It seems to depend on certain circumstances, as the condition of the station, the softness or moistness of the ground, etc., and I think it very probable that the stolons might be transformed, or rather developed, as runners by being kept out of the ground and prevented from bending downwards under the surface of the earth. In every case, as it will be shown later, their structure is almost the same as that of the runners.

The stolons consist of several internodes, the length of which varies from less than 1 centimeter to 5 or 6 centimeters; they are white, translucent, and bear at each node a very small, scale-like sheathing leaf, cleft a little above its middle, as is shown in Plate XLVI, Figs. 3-4, where such a leaf is drawn from two sides, and under these leaves can be seen some very small and thin roots, which are often but slightly branched.

At the end of each stolon we see (Plate XLVI, Fig. 8) a tuber, of which the first internode is almost cylindrical, elongated, and usually about one-half centimeter in length, and longer than the other internodes of the tuber. The figures 8-11 on Plates XLVI and XLVII show four tubers of different sizes and states of development. The largest one (Fig. 10) had a length of 1½ centimeters, but this size is exceptional, as they are usually not longer than 1 centimeter. The number of internodes varies from two to six, but four is the most common. These internodes are cylindrical, often a little broader at the middle, and are yellowish-white in color. They are all provided with leaves, closely pressed to the nodes, and these leaves are scale-like, but always cleft to the middle, with the lobes ovate and nearly obtuse (Plate XLVII, Fig. 12). Usually three to five roots are to be seen under these leaves, which are in the young tubers developed, but as small warts, but later, by the germination of the tuber, they grow out and attain a development as small, thread-like roots, with only a few ramifications.

At the end of the tuber we see a conical bud, often somewhat pointed, and usually directed a little upwards, and this bud is able to develop an independent plant in the following spring, while the stolon is not persistent, but dies a short time after the formation of the tuber, during the fall or in the beginning of the winter. But, besides this bud at the end of the tuber, we find one in the axil of each tuber-scale, which is only developed as a small protuberance, which may develop into short-stalked tubers, or, more correctly, short stolons with tubers at their end, as it is shown on Plate XLVI, Fig. 7. It does not happen very often, according to the plants I have had the opportunity of examining, that these buds become so developed, but I should suppose that they are nevertheless of some importance for the propagation of the plant, if the tuber should be injured and the terminal bud destroyed. The impor-
tance of these stolons with their tubers must be very considerable for the propagation of the plant; but besides these tubers, with all their buds, we can find also in the axils of the leaves of the stolons small buds, which are not only able to develop lateral branches, ending in tubers, but also in some cases, as shown (Plate XLVI, Fig. 6), a short branch with leaves of the same shape as those belonging to the stem. The development of buds in this manner does not seem to be common, but I have found it in some of the specimens collected along the Eastern Branch. How far such a small branch may be developed I do not know, but some of them showed, besides the leaves, also some very young flowers, not perfectly developed, of which especially the calix and the corolla were rudimentary or almost wanting, not unlike what are called "clandestine flowers," but it is hardly probable that they are to be so considered. There is, then, in the stolons a certain ability of taking on the function of the runners also, by developing leaves and flowers, though these are not completely developed in the present case; but on the other hand it must be remembered that they were found under ground, therefore it seems that, had the conditions been better, they might have attained a more perfect development.

The other method of vegetative propagation in Hydrocotyle Americana is by runners. These are developed from the axils of the leaves of the upper part of the stem, as shown Plate XLVI, Fig. 2, and they attain frequently a length of 16 centimeters. They are translucent and have long internodes like the stolons, but are a little thicker than these, and bear leaves of the same shape as those of the stem, only proportionally shorter stalked. No buds were developed in the axils of these leaves, or at least not in the state in which I had opportunity of examining them.

Roots are developed under the leaves, but they seemed to be very weak, and this circumstance, in connection with the somewhat feeble development of the runners, does not make it probable that very extensive propagation takes place in that manner. The function of the runners is to form new plants when they are provided with roots at their nodes, and thereby creeping on the earth. But I have not been able to find a single young plant originating in this manner, and it does not seem probable that the runners could resist the frost of winter. Possibly their character as runners depends on the circumstance that they have not been able to bend themselves downwards before their long internodes were developed, and that they might not have been strong enough for penetrating the ground with their ends; for, as we have seen, they are only to be observed in the axils of the upper leaves of the stem. This last circumstance seems certainly to speak in favor of the supposition, owing to their character as merely runners; for the stem of our plant is a little ascending; so that only the branches from the lower-situated leaves can reach the ground pretty soon, while it must be necessary for those from the axils of the upper leaves, the
higher situated, to stretch themselves for reaching the ground, and I believe that the most natural and for the plant the most useful development of these branches from the axils of the leaves should be if they all were developed as tuberiferous stolons.

In regard to the internal structure of these organs, we see in the stolons a very distinct cuticula, showing several frownings, an epidermis of which the exterior walls of the cells are somewhat thick, while the interior ones are thinner, and show a development almost as collenchyma (Plate xlvii, Fig. 15). Stomata are present, but merely in a small number. Inside the epidermis there is a bark composed of parenchyma, with large cylindrical cells with very thin walls. There are usually six vascular bundles, with a distinct duct, apparently merely containing air, outside the phloëme, and there is no indication of any mechanical tissue either forming a sheath or isolated groups. The cells of the pith have the same shape and size as those of the bark. Starch is present in the bark, but is only to be observed in the younger state of the stolons; not at all by the older ones.

The structure of the runners is almost the same as that of the stolons, except that the stomata are more frequent; the cuticula does not show frownings, and the cells of epidermis have thinner walls. The bark and pith show the same structure, and the vascular bundles are stronger developed and the groups of phloëme and xyleme larger. The ducts outside the phloëme are also present in the runners.

The stem shows the same general structure, but the cells of the epidermis have attained a still greater thickness, and we find inside these a stratum of cells of an almost collenchymatous character (Plate xlvii, Fig. 14). Otherwise the structure is the same as that of the runners.

The complete want of mechanical tissue in the stolons and runners seems to indicate that their persistence can not be very long, and their anatomical structure shows a very uniform development in both.

As to the structure of the tubers, we find that a transverse cut of a young tuber, formed this year, shows a large amount of starch, deposited in the bark and pith, and in such a manner that its presence perfectly conceals the structure of the different strata of cells. But we may see, however, very distinctly usually six concentric rather large ducts, and these are of the same kind as those mentioned above. A transverse cut of an old tuber (Plate xlvii, Fig. 16), which has developed a plant, and therefore has been deprived of its starch, shows the structure much better. The cells of the epidermis do not show any essential difference from those of the runners, the structure of the bark and pith corresponds perfectly to the description given before, and the development of the vascular bundles is very uniform. The ducts are to be seen outside the phloëme, as in the stem, the runners, and the stolons; but outside these we find an endodermis, forming a ring around the vascular bundles, and whose cells show very thin walls, but somewhat indis-
tinctly the spots called after Caspary. No indication of mechanical tissue was to be observed in the tuber.

If we now turn to the description of our plant as given by the early authors and compare it with what has been shown here, we shall find that Michaux’s "radice tuberosa" is to be regarded as an old tuber that has developed a plant, and Pursh’s "herba glabra tuberosa" shows the same, and evidently he had seen more than a single tuber, since he has described not only the "radix" but the plant as being "tuberosa," and we suppose the same of Eaton’s "tuberous." But as to the description of the stolons and runners, it is not sure whether what Torrey describes as "suckers" should be regarded as stolons or not, when a sucker, according to Gray’s "Structural Botany," 1880, is "rising from a subterranean creeping base," and, as it has been shown above, our plant has no "suckers." "Darlington’s filiform runners, from the axils of the leaves," may be nothing but the true runners; but, on the other hand, he does not mention if he has observed them in the axils of the upper leaves or where, and it might not be improbable that he had seen the base of the stolons also, but with the tubers broken off. Chapman’s "stoloniferous" seems certainly to show that he has observed the presence of the true stolons, and it is a question why he did not mention the runners.


EXPLANATION OF PLATES.

Hydrocotyle Americana L.

PLATE XLVI.

Fig. 1. The lower part of the plant, developed from a tuber, with stolons ending in tubers.
2. The upper part of the plant, with two runners.
3. A scale-like leaf from a stolon, seen from the front and back. R., roots.
4. A scale-like leaf from a stolon, supporting a branch with its first leaf L. R., roots.
5. A scale-like leaf from a stolon, supporting a branch with a leaf of the same shape as those of the stem. R., roots.
6. An old tuber, having developed a plant. Two stolons, ending in tubers, are to be seen, of which the one has been developed from the axil of the uppermost scale-like leaf of the old tuber.
7. A young tuber of the most common shape.
8. A young tuber just formed.

PLATE XLVII.

9. A young, very long tuber, consisting of six internodes.
10. A young tuber with a smaller one, developed from the axil of one of the lower-situated scale-like leaves.
11. Leaf of a tuber.
12. The development of a stolon, at the summit of which the bicleft leaf is to be seen.
Fig. 14. Transversal cut of a stem. Ep., epidermis. B., bark. D., the duct outside the phloëme. P., pith.
15. Transversal cut of a stolon. Ep., epidermis. B., bark. D., the duct. P., the pith.
17. A duct, D., of an old tuber.