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BIOLOGICAL NOTES ON CANADIAN SPECIES OF VIOLA.

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(With two plates, drawn from nature by the author.)

In recent years North American, and especially Canadian, violets have attracted considerable attention on account of their very liberal contributions to the number of "undescribed species"; but it so happens that we have gained no further knowledge of the life-history of the genus than we already possessed from the time when the *Violaceæ* were studied from a thoroughly scientific point of view, when species were studied and treated as living beings with some power to adapt themselves to their environment and to vary, instead of as mere unnamed herbarium material. It really seems as if the species of *Viola* fared better at the time of Linnæus than they do now, for at that time they were at least classified in such a way as to become readily determinable, while in recent years the accumulation of supposed new species has gone on so rapidly as to leave the enumeration of these in anything but a systematic arrangement, with the omission of important morphological characters and regardless of natural affinities.

We naturally arrive at the conclusion that it would be more desirable and more beneficial to the study of natural science if we contented ourselves with a smaller number of species but well-defined and better appreciable from a biological view-point. The mere leaf-outline, the presence or absence of pubescence, the relative size and color of the perfect flower are deceptive characters, and even the position of the so-called "apetalous" flowers: aerial or underground, is far from constant. Systematic works, even of a very recent date, seldom contain anything new in the line of biology or morphology, since the authors generally content them-

selves with reproducing diagnoses that have been published long ago, instead of submitting the plants to a renewed study, whereby surely some new characters would be discovered; the only thing "new" to be found in such systematic works seems to consist in nomenclatorial changes: new combinations and new genera, based on specific rather than generic characters.

It is therefore to be hoped that Canadian botanists will undertake the work of studying such plants of their own, which need a revision, and, for instance, the *Violaceæ* would no doubt prove to be interesting from a biological view-point, besides that a close study of the various organs might reveal new characters of importance to the distinction of several critical species.¹ Some of these characters may be sought in the structure of both the perfect and cleistogamic flowers, in the leaf-variation, the structure of the rhizome and in the development of root-shoots. Having studied the genus from time to time, the writer thought that the publication of some observations upon the structure of these organs might be of some interest to Canadian botanists, besides that these notes might indicate the line of work to be pursued. We might begin with

THE FLOWERS.

Two kinds of flowers are known to occur in the genus *Viola*: the perfect, which we know is to be found in all the species, and the cleistogamic, which is far from uncommon, but which, nevertheless, seems characteristic of certain species, or perhaps better of certain sections of the genus; it is absent in *Viola pedata* and *tricolor* for instance. The perfect flower is, as we remember, hermaphrodite and zygomorphic, *i.e.*, symmetry in one plane; the sepals are prolonged backwards beyond their point of insertion, they are glabrous or hairy, often ciliate, and we have noticed much variation in their shape and in the length of their appendages; the corolla is polypetalous with the anterior petal larger and, sometimes, of a different outline from the others,

¹ The very work suggested by Dr. Holm is now being carried on at the Central Experimental Farm by Dr. James Fletcher, who has under cultivation there all the Ottawa species and many from other parts of Canada. The results of Dr. Fletcher's studies will doubtless be given to the Club when they have been completed.—EDITOR.

besides that it bears a spur of variable length. The five stamens are closely applied to the ovary ; they have short filaments, and at their summit generally a membranaceous appendage formed by the prolongation of the connective ; the two anterior stamens are provided with a spur-like nectary, which protrudes a considerable distance into the petaloid spur ; this nectary shows several modifications in North American species and ought to be studied and described in the diagnoses. Finally, the ovary has a club-shaped style and bears the stigma in a groove on the anterior side.

These perfect flowers are, however, far from being always fertile, and it appears, from our own observations, as if they are sterile in a number of the acaulescent, purple-flowered species, at least in the vicinity of Washington, but whether these same species behave in the same way further north would be worth while determining. The other kind of flower, the cleistogamic, is often, but very incorrectly described as "apetalous," evidently from the fact that it has not hitherto been carefully examined in this country. The term "cleistogamic" is thus designated to such flowers as remain closed, in which the petals are merely present as rudiments or, sometimes, totally absent, and in which the stamens are reduced in number, besides that their anthers are small and contain but a few pollen-grains, which generally emit their tubes while still enclosed in the anther-cell. The pistil is in these flowers smaller than in the perfect ones, and the stigma is often scarcely developed. These flowers nevertheless produce a larger quantity of seeds than the perfect, and they have, in a number of cases, the power of burying themselves in the ground, where the seeds thus become ripened, or they are borne on erect, aerial peduncles like the perfect flowers.

Cleistogamic flowers are known from very nearly sixty genera, especially among the *Papilionaceæ*, *Acanthaceæ*, *Malpighiaceæ*, in certain species of *Oxalis*, *Lamium*, *Linaria*, *Drosera*, *Viola*, etc., while they are rare among the *Monocotyledones* : *Juncus*, *Hordeum*, *Leersia*, *Amphicarpum*, *Commelina*, etc.¹

In the genus *Viola* these flowers were known already to Dillenius and Linnæus, which is readily to be seen from their

¹ Compare Darwin : Different forms of flowers, p. 310.

diagnoses of *V. mirabilis*: "*Viola montana latifolia*, flores ex radice, semina in cacumine ferens Dill.," and "*Viola floribus radicalibus abortientibus, caulinis apetalis seminiferis* Linn." But besides *V. mirabilis* a few other old world species of the genus are known to produce cleistogamic flowers as, for instance, *V. odorata*, *silvatica*, *canina* and *persiæfolia*, some of which have been described and figured by Professor Warming in his Manual of General Botany (1895. p 546.). The structure of the cleistogamic flowers is not, however, identical in all the species, and in regard to the North American species we have noticed some peculiarities, which may prove useful in the distinguishing of certain species.

The cleistogamic flowers remain constantly closed in the species which we have examined, and the general aspect is like that of *V. Macounii*, figured on our Plate IV, fig. 1, and the flower is nodding like the perfect. The sepals are normally developed and show a very prominent ciliation, but the petals are merely present in the shape of small warts; only two stamens are developed, (fig. 2) and in their natural position they are closely applied to the pistil. These stamens have large connectives, prominently denticulate along the margins, and the anthers are small and contain as usually only a few pollen-grains. The pistil has a short curved style, but no proper stigma is developed. These cleistogamic flowers of *V. Macounii* are sometimes buried in the ground, but at other times they are raised above the surface, borne on almost erect peduncles. It seems as if this varied position is due to atmospheric conditions; we have at least noticed that in several other species these flowers are only buried in the ground when the season is very warm and dry, while they develop above ground when the atmosphere is damp and cool. In *Viola papilionacea* the cleistogamic flowers are, thus, not always underground, and they differ from those of *V. Macounii* by having larger appendages on the sepals (fig. 5) and by these being glabrous. In this species there are, also, only rudimentary petals and only two stamens, which are somewhat larger than those of the former species. But in *V. sagittata* the cleistogamic flower is very much different. The appendages of the sepals (fig. 8) are long and narrow; the anterior petal is plainly developed

(fig. 9), and there are three stamens (fig. 12), of which, however, only two have both anther-cells developed. One of these stamens has always, as in the preceding two species, the connective folded around the style and stigma, as shown in figure 10, and the structure of the anthers and the connective is identical. The cleistogamic flowers are in this species, *V. sagittata*, constantly raised above ground on erect peduncles of quite considerable length, and it appears as if the position of these peculiar little flowers might constitute, if not a specific, then at least a sectional character. And in looking over the several species in which cleistogamic flowers occur, we notice that some of the acaulescent, woodland types: *V. papilionacea*, *Macounii*, and *villosa* show a tendency of burying the flowers in the ground, while the bog plants: *V. sagittata*, *blanda*, *lanceolata*, *primulæfolia*, *affinis* and *cucullata* always bear the cleistogamic flowers on erect peduncles; on the other hand, *V. emarginata* and *ovata*, both inhabitants of sandy, gravelly hill-sides, bear the flowers raised above the ground. This varied position observed in the cleistogamic flowers depends evidently upon the character of the substrate: humus, wet boggy ground or gravelly soil, besides that, the atmospheric conditions may not be excluded. If the flowers and fruits of the bog species were buried in the wet moss, they would, no doubt, be exposed to decaying, and it seems very natural that *V. affinis* always bears these flowers raised above ground, when it occurs in swamps or wet meadows, while it partly buries them in the ground, when growing in thickets, border of woods, etc.

Very peculiar is the mode of growth observed in *V. rotundifolia*. The perfect flowers are in this species plainly developed from the axils of the basal leaves: acaulescent, while the cleistogamic are borne in the axils of cauline leaves: caulescent; it appears as if the stems which bear the cleistogamic flowers in this species are mostly subterranean, but we have seen one instance, however, where a stem bore a few green leaves instead of merely scale-like. In *Viola orbiculata* it is interesting to see that two sets of aerial stems with green leaves and flowers develop in the same season, and that the flowers of the first set are perfect and very showy, though sterile, while the later developed are all cleistogamic and closed, but produce seeds.

While thus cleistogamic flowers appear to be common to a number of species of *Viola*, there are certain North American species in which they are absent, for instance, *V. pedata* and *rostrata*. In *V. striata*, *Canadensis*, *pubescens* and *glabella* we have observed a few instances where the last developed flower was merely rudimentary, but with no signs of producing any seeds, while such were produced by all the perfect ones on the same stem. And in *V. sarmentosa* we have not succeeded in detecting a single cleistogamic flower in our herbarium specimens, and not in *V. Langsdorfi* either. We hope, however, that Canadian botanists will re-examine these species in the field, more especially the two last mentioned, since it is very important to learn something about the structure of the cleistogamic flowers in general in others than those described above

VARIATION IN LEAF-OUTLINE.

When numerous leaves develop from the same bud as in the monopodial, acaulescent violets, certain variation becomes always more or less noticeable in the leaves. Those that develop first, before the flowers, are frequently different from the later ones, and in certain species, *V. papilionacea* and *palmata*, for instance, the first of these are generally cordate or reniform, but entire, while the later ones, sometimes, are more or less deeply lobed. In *V. sagittata* the variation in leaf-outline is quite considerable, and we have, sometimes, noticed a number of forms upon the same individual during one season, from the oblong-ovate to the lanceolate, with the base hastate, or from the deltoid, entire to the deeply lobed, the latter being characteristic of the so-called *V. emarginata*. Such variation seems largely due to the position of the leaves in the bud, but there are, also, cases where the nature of the surroundings seems to affect the leaf-shape. *Viola emarginata*, for instance, does not develop the deeply cut leaves except when it grows in rich soil and in shade; in open places and in sandy soil the leaves become entire and often quite narrow like those of *V. sagittata*. *V. palmata* has always the later leaves deeply lobed, when growing in woods, while *V. papilionacea* shows a pronounced lobation, when observed in damp, shaded places, along creeks, etc.

The caulescent violets show but a slight variation, which is restricted to the mere serration or crenulation of the leaf margin. But the most conspicuous variation is to be observed in *V. pedata*, if we compare the leaves of the mature plant with those of the rootshoots. Some of these types of leaves are figured on our plate (Plate V, figs. 13-16), and we notice the great divergence between the normal leaf (fig. 13) and the smaller one (fig. 14), which was taken from a one year old specimen. In the rootshoots (figs. 15-16) the leaves show a tendency to becoming almost entire, and one would hardly have suspected them to belong to this species, if it were not for the fact that we succeeded in preventing them from breaking off when the mother-plant was lifted.

Considering these few but well marked cases of leaf-variation in *Viola*, we might suppose that several of the recently described new species, in which the outline of the leaf constitutes an important part of the diagnosis, may be referred to some single type with ability to adapt itself to the surroundings, and to exhibit a certain amount of variation. And we must remember that besides varying in leaf-outline these same species do, also, vary in respect to the pubescence, which is still more influenced by the conditions of the surroundings, character of the soil, light and shade, etc., and it can, of course, only be ascertained through prolonged study in the field whether such plants are sufficiently constant in their mode of growth so as to be considered as valid species.

THE RHIZOME.

Few organs are as constant in their structure as those which constitute the rhizome, the under-ground stem-portion, with its leaves and roots; yet it is very seldom that recent authors pay much attention to this part of the plant, when they describe new species; in regard to *Viola* it is generally passed by in silence. The following types of rhizome are observable in the Canadian perennial species of *Viola*:

- A. Rhizome vertical, monopodial, leaves all basal with axillary flowers:

V. pedata.



B. Rhizome horizontal, otherwise as in A :

V. sagittata, affinis, Macounii, cucullata, palmata, papilionacea.

C. Rhizome horizontal or ascending, monopodial, with basal leaves from the axils of which aerial stems develop with leaves and flowers, but no stolons :

V. pubescens, glabella, orbiculata.

D. Rhizome a sympodial pseudorhizome with basal leaves, etc., as in C :

V. Canadensis, striata, rostrata.

E. Rhizome horizontal, monopodial, leaves all basal with axillary flowers and stolons with scale-like leaves :

V. Leconteana, primulæfolia, Selkirkii, blanda, lanceolata.

As may be readily seen from this table, the monopodial ramification seems the most characteristic, while the sympodial occurs only in a few species. Of these two kinds of branching, the monopodial is in *Viola* recognized by its continuous growth in one direction and by its terminal bud developing only leaves with axillary shoots : floral or vegetative, of which the latter continue the same development of leaves and without being terminated by a floral axis. These lateral shoots, however, do not attain the same length or the same strength as the mother axis, unless in cases where this becomes injured and dies off. It is thus characteristic of the monopodium that the terminal bud remains vegetative and for an indefinite period.

The sympodial rhizome is in *Viola* but sparingly represented, and as a matter of fact it does not occur as a true rhizome in the stricter sense of the word. We have called it a pseudorhizome, because the under-ground stem-portion is here (in *V. Canadensis*, etc.) only represented by the bases of the aerial shoots, from the lowermost leaf-axils of which buds develop, which in the following season grow out into above-ground shoots. But there is no under-ground mother-axis in these species, and, moreover, each bud becomes terminated by a floral shoot with cauline leaves and axillary flowers. And it is seen without much difficulty when we examine *V. Canadensis* that the fresh, flowering shoots are, always, borne upon the base of an old, withered stem from the previous year. One might suppose that *V.*

pubescens, *glabella* and *orbiculata* ought to be reckoned of the same group as *V. Canadensis*, but in these species as well as in the more southern *V. hastata*, the above-ground stems are readily seen to have developed directly from the rhizome and in the axils of leaves, pertaining to the terminal bud. In other words, their rhizome represents a monopodium just as typical as the one described above, with the only difference that in the one case only flowers develop, while flower-bearing stems develop in the other. These flower-bearing stems die down to the ground without leaving any basal buds for reproduction; this is secured by the terminal bud of the under-ground main-axis.

In *V. pedata* the rhizome is constantly vertical; it is rather short, but quite thick, and the primary root persists for about two years. In *V. papilionacea*, *affinis*, etc., the rhizome is horizontal, somewhat longer, but the internodes are barely visible. The thickness of the rhizome is in these species (B) as well as in *V. pedata* due to the swollen bases of the petioles, as we have described in a previously published paper.¹ In *V. primulæfolia* and its allies (E) the rhizome is quite slender, and these species are characterized by their more or less profuse development of long, very slender, subterranean stolons, each of which becomes terminated by a rosette of leaves like the mother-shoot, and in which the same monopodial branching takes place.

The peculiar instance of both caulescent and acaulescent flowers developed upon the same rhizome is illustrated by *V. rotundifolia*, as described above. However, our material was rather scant of this species, thus we were unable to make out whether the cleistogamic flowers are borne on stems that are aerial or subterranean under normal conditions.

In *V. sarmentosa* we have a type which is very different from all the others on account of its sarmentose habit. The stolons are, as it appears from our dried material, always above ground, inasmuch as they all bear typical stem-leaves, but scattered, not forming a rosette as in the monopodial species. None of our specimens showed any rhizome, but they were all developed from stolons, which had rooted and become separated from the mother

¹ Memoirs of the Torrey Botanical Club. Vol. 2, No. 3, p. 66.

plant. Canadian botanists are urgently requested to study this species in order to explain its mode of growth from young to adult stage, and especially to demonstrate the structure of the rhizome and of the cleistogamic flowers, if such are present.

In comparing the rhizomes of these Canadian violets with European species, it is interesting to notice that there is only one, *V. mirabilis*, which exhibits the same growth as *V. rotundifolia*, and that these two species are not to be considered as near allies, since the former has the flowers light purple, the latter, on the contrary, yellow. In *V. odorata* the rhizome is monopodial and the flowers as in our acaulescent species, but there are also runners, which stay above ground and which develop rosettes of leaves at their apex, thus repeating the growth of the mother-rhizome. The caulescent *V. sylvatica* and *V. Riviniana* agree in all respects with *V. pubescens* and its allies, while the pseudorhizome of *V. Canadensis* is readily recognized in the European *V. canina*, *stagnina*, *elatior* and a few others, which have been described by Professor Hjalmar Nilsson.¹

THE ROOTS.

The primary root persists for about one season in these perennial species of *Viola*, but is soon replaced by adventitious, which in the monopodial types develop from the base of the petioles from four to five together, or scattered along the internodes of the stolons, as in *V. primulaefolia*, etc. These roots are usually of two kinds: nutritive and storage, of which the latter are quite common in the monopodial species of the groups A, B and C; they are not very thick, however, but possess, nevertheless, a large parenchymatic tissue of the cortex with an abundance of starch, and correspond well with this type of root as described by Dr. Rimbach.² No contractile roots were observed.

THE ROOTSHOOTS.

This form of shoot has only been observed in *V. pedata*, as described above, and we might state here, that the shoots develop at the tips of the roots and that they remain in connection with

¹Acta Universitatis Lundensis. Vol. 19. 1882-83, p. 205.

²Berichte deutsch. botan. Gesellsch. Vol. 17. 1899, p. 18.

the mother-plant for at least two seasons; they commence to bloom in their second year. But in no other American violet have we, so far, detected rootshoots, and they are not very well known among the old world species either. Wydler and Irmisch noticed them in *V. sylvatica*, *Riviniana* and *canina*, and Professor Warming found them in *V. elatior*.¹ It would seem that they might be found among the corresponding American homologues, viz.: *V. Canadensis*, *striata* and *rostrata*, and perhaps also in the species of the group C.

In considering the means of propagation, floral and vegetative, as possessed by these Canadian species of *Viola*, it seems as if those of the group E (*V. primulæfolia*, etc.) are the best equipped, since they produce stolons and develop seed-producing flowers besides; these species are, thus, able to wander and spread themselves over a larger area than the others, in which stolons do not occur. *Viola pedata*, with its short and plump, vertical rhizome, is, nevertheless, possessed of some power to wander by means of the rootshoots. But in all the other groups (B, C and D) the structure of the rhizome does not enable the individual to spread over any large area, and the principal distribution is in these species secured by the seeds, which are ejected with much violence and thrown to a great distance by a peculiar mechanism of the carpels. This manner of dispersing the seeds becomes, of course, much impeded when the cleistogamic flowers bury themselves; it may be for this same reason that the bog-species have their pods raised high above the wet, mossy substrate, by which the dispersion of the seeds become better secured than otherwise.

Brookland, D.C., September, 1903.

EXPLANATION OF PLATES.

PLATE IV.

Fig. 1—*Viola Macounii*. A cleistogamic flower, magnified.

Fig. 2—Same species. A cleistogamic flower laid open, showing five sepals, rudimentary wart-like petals, two stamens and the pistil, magnified.

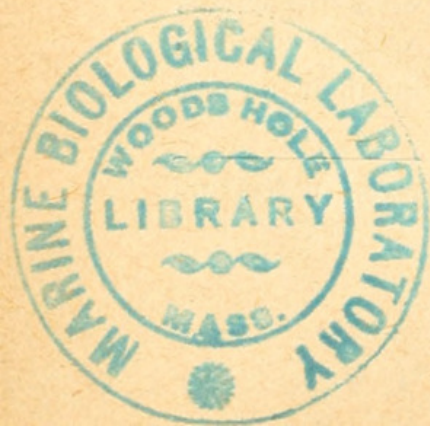
Fig. 3—Same species. The pistil and the two stamens in their natural position, magnified.

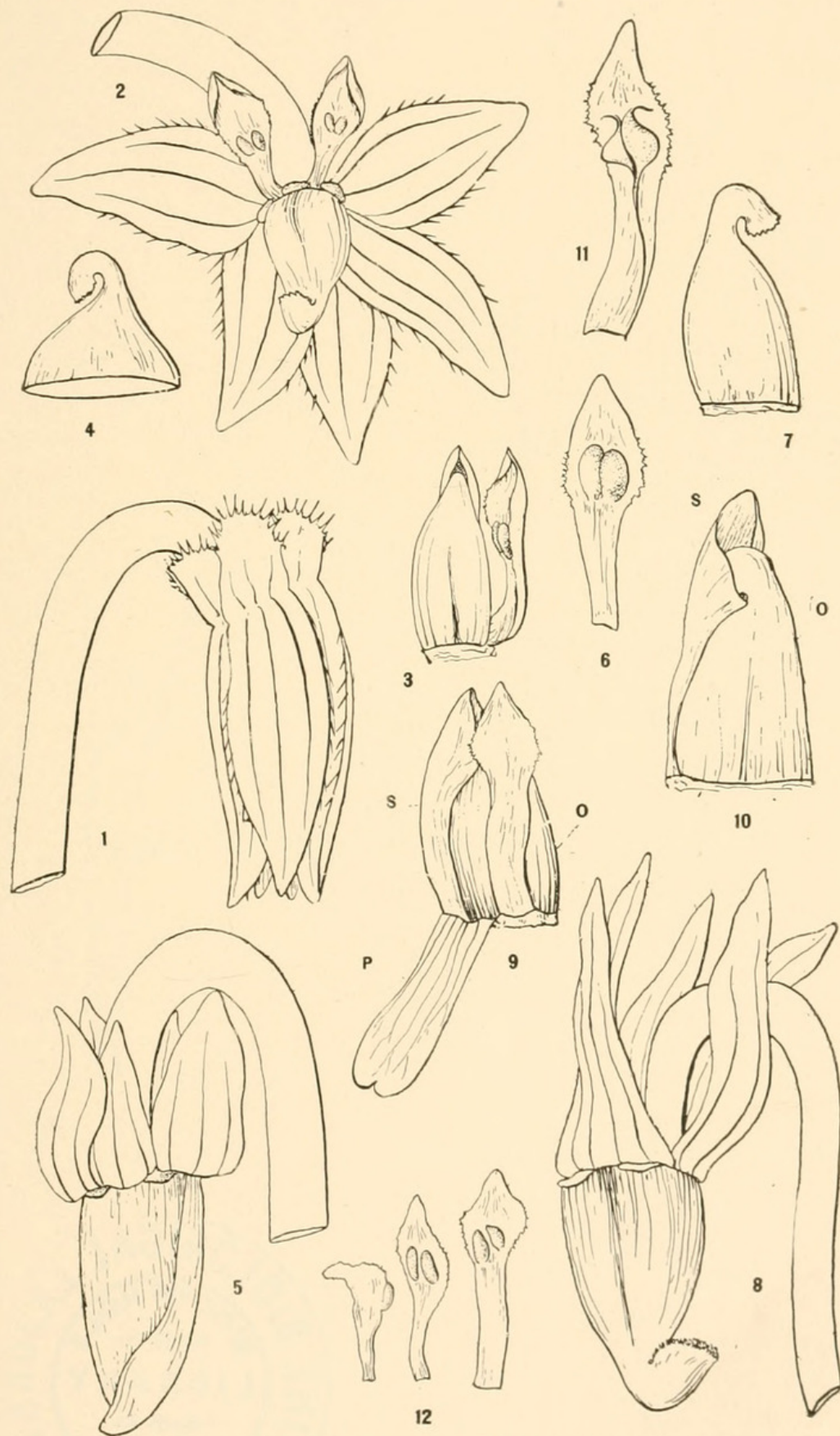
¹ Botan. Tidsskr. Ser. 3. Vol. 2. Copenhagen, 1877-79, p. 63, and Botan. Notiser. Lund., 1884, p. 32.

- Fig. 4—Same species. The apex of the pistil with the style and stigma, magnified.
- Fig. 5—*Viola papilionacea*. A cleistogamic flower, with the sepals, excepting the appendages, removed; the petals are represented by small, wart-like organs, and the stamens are closely applied to the pistil, magnified.
- Fig. 6—Same species. A stamen showing the two anther cells and very large, ciliate connective, magnified.
- Fig. 7—Same species. The pistil, magnified.
- Fig. 8—*Viola sagittata*. A cleistogamic flower showing only the long appendages of the sepals and the pistil, magnified.
- Fig. 9—Same species, showing a small petal, the anterior, two stamens and the pistil, magnified.
- Fig. 10—Same species. The pistil and a stamen, magnified.
- Fig. 11—Same species. A stamen with the anthers very irregularly opened, magnified.
- Fig. 12—Same species. The three stamens of the flower, magnified.

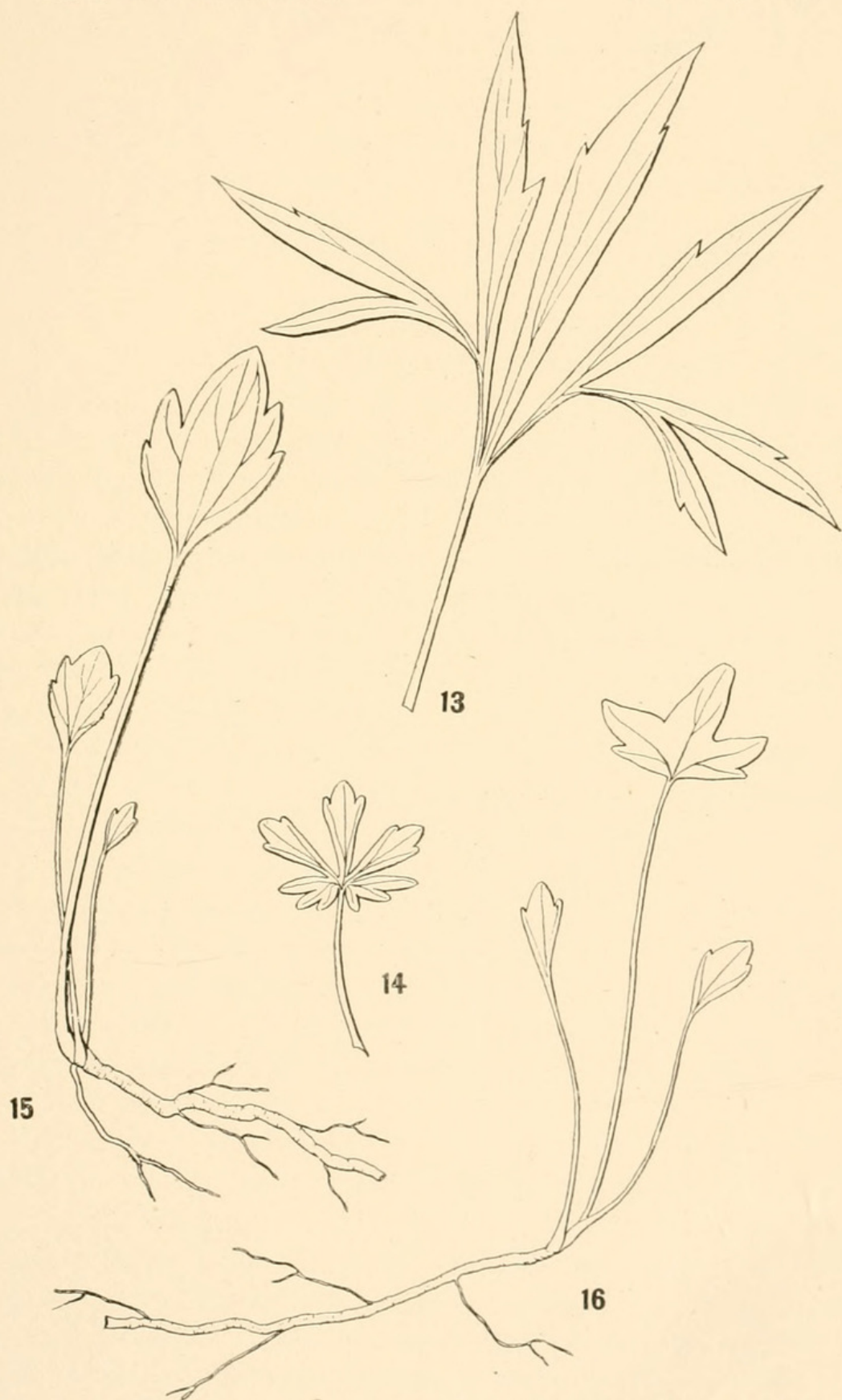
PLATE V.

- Fig. 13—*Viola pedata*. A typical leaf, of an old specimen collected in the month of August. Natural size.
- Fig. 14—Same species. A leaf, one of the earliest developed, of a young specimen, one year old, collected in the month of April. Natural size.
- Fig. 15—Same species. A rootshoot, collected in the month of June. Natural size.
- Fig. 16—Same species. A rootshoot, collected in the month of June, showing various forms of leaves. Natural size.
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Holm: Notes on Violets. Cleistogamic flowers.



Holm ; Notes on Violets. Leaves and root-shoots of *Viola pedata*.



Holm, Theodor. 1903. "Biological Notes on Canadian Species of Viola." *The Ottawa naturalist* 17(9), 149–160.

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