

ART. XXXV.—*Method of Hibernation and Vegetative Reproduction in North American Species of Stellaria*; by THEO. HOLM. (With six figures in text, drawn from nature by the author.)

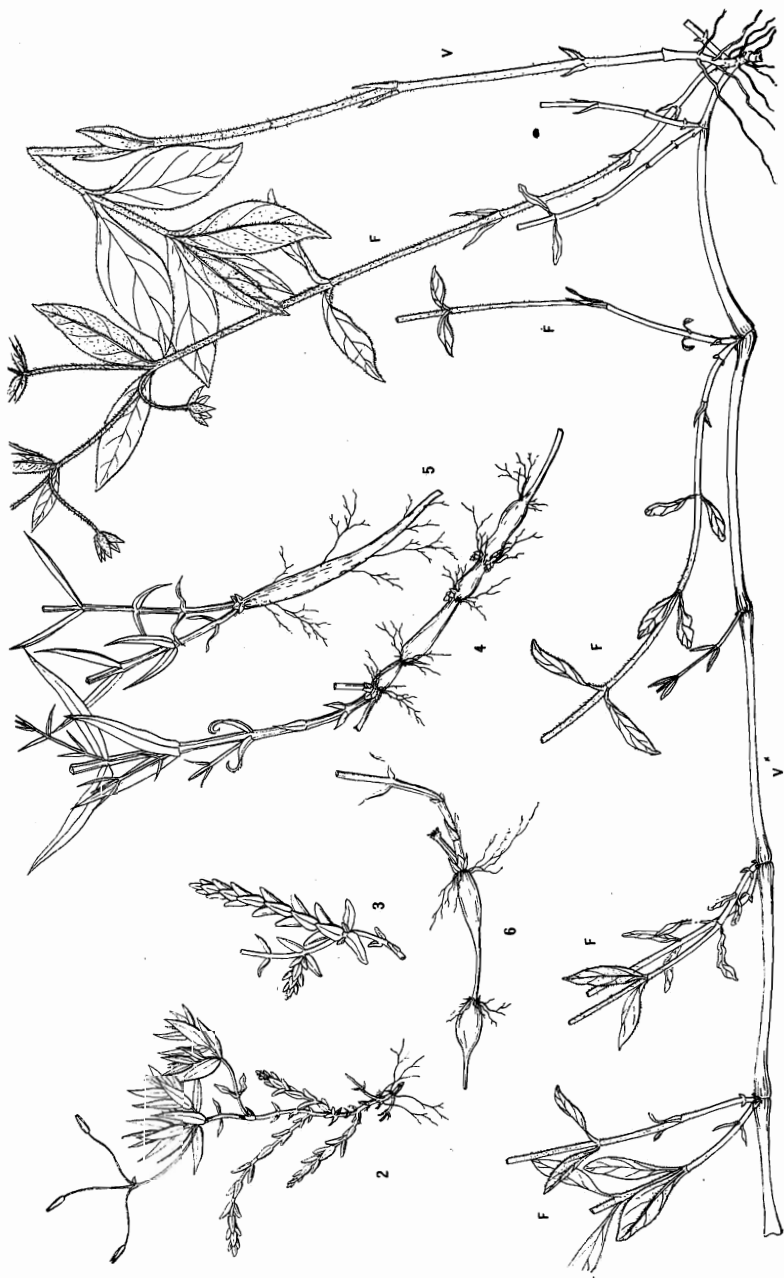
ALTHOUGH the *Caryophyllaceæ*, and especially the *Alsineæ*, exhibit such a remarkably wide geographical distribution throughout the northern hemisphere, being able to thrive in the most northerly points* and at the highest elevations† at which flowering plants are known to exist, they are, nevertheless, rather poor in biological types.

Neither the aerial nor the subterranean organs have become modified to any great extent that might lead us to suspect the extraordinary vitality possessed by some of these species. The habit is strikingly uniform; the diagram of the flower, the structure of the inflorescence, the foliage, and the ramification of the shoot is almost identical, or at least very little modified in a number of these plants. In the perennial *Sileneæ*, for instance, the frequent structure of the shoot with its compact rosette of leaves and persisting primary root shows very little variation among the arctic, the alpine, and lowland representatives; among the *Alsineæ* we observe in some genera exactly the same morphological structure as in the *Sileneæ*, while in others there is a marked tendency to spread by producing creeping rhizomes so as to enable the individual to take rapid and wide possession of the soil. In the genus *Stellaria*, for instance, there are some perennial species, in which the shoot demonstrates certain characteristic modifications so far as concerns "hibernation and vegetative reproduction," and these we intend to illustrate by a few examples, inasmuch as the literature does not give but a very scant information about the biology of these plants. The diagnoses of the species as given in the Synoptical Flora‡ are undoubtedly very exact, and may be sufficient for the determination, but mostly the floral organs have been considered; we believe, however, that the vegetative organs in several cases might be of some importance also, not only as a means of distinguishing the species, but also for the sake of giving a more complete demonstration of the particular habit of some of these plants.

* *Cerastium alpinum* L. has been collected at 82° 50', *Stellaria longipes* Goldie and *Alsine verna* Bartl. at 82° 27', and *Alsine Groenlandica* (Retz.) Fenzl at 81° 42' N. L.

† *Arenaria Stracheyi* Hook. grows at an elevation of 19,200 ft. in Tibet; *Cerastium trigynnum* Vill., *Stellaria subumbellata* Edgew., and *Sagina procumbens* L. are reported from the Himalayas at an elevation of 16,000 to 17,000 ft.

‡ Fasc. II, p. 208, 1895-97.



So far as concerns the perennial North American species of *Stellaria* s. s. (not including *Malachium* and *Cherleria*) the primary root is only of short duration, but becomes replaced by secondary roots developing from the basal nodes of the aerial stem or from the rhizome. Very characteristic of several of these species is the ability of the stems above ground to remain active for more than one season, beside that some of these are, moreover, provided with true rhizomes; in one species we find the shoots to be differentiated as floral and vegetative, the former being merely annual, while the latter may persist for about two seasons. Finally in another species we notice a highly developed rhizome with fleshy, swollen internodes, resembling long tubers. We might thus distinguish between these types so far as concerns the vegetative reproduction, viz:

A, without rhizome, but with persisting aerial stolons.

B, with rhizome, and with persisting aerial stems.

C, with rhizome, but without persisting aerial stems.

Of these the first type is represented by *Stellaria pubera* Michx. and may be described as follows:

Stellaria pubera Michx.

The plant is generally in full bloom in April or in the earlier part of May; the floral shoots are quite numerous, spreading, and leafy to the top. The inflorescence is a regular, very rich-flowered cyme. About the middle of May, or even earlier, while the plant is still blooming, a few vegetative shoots commence to develop (V in fig. 1). The leaves of these shoots are always larger than those of the floral, but otherwise in regard to pubescence and outline the foliage is the same.* It is now interesting to see, that while the floral shoots die down to the ground as soon as the fruits have matured, the vegetative shoots not only remain active, but they continue their growth for several months with the leaves fresh and green. Sometimes a few-flowered inflorescence develops at the apex of these shoots, but it seems to be the most frequent case that they stay as purely vegetative. Although these flowers become developed much later than the others (those of the normal, floral shoots), they are, nevertheless, perfect, and of the same size or even larger than the earlier ones. If we examine the plant in the month of August or early in September, we find the vegetative shoots still alive, but closely appressed to the

* As stated in the Synoptical Flora, p. 236, "the stems are pubescent in lines" mostly so, but not always; in the vicinity of Washington, D. C., it is not uncommon to find individuals as the one figured (fig. 1) in which the pubescence is not in lines but equally distributed all over the stems and branches of the inflorescence.

ground; then the leaves begin to wither, and nothing will be seen of the plant until next spring. We have, thus, in *Stellaria pubera* two kinds of shoots: floral and vegetative, of which the latter remain active for a much longer period than the floral, and of which the function is to give rise to new individuals. This may be readily observed during the spring, by lifting the plant carefully.

As shown in our figure 1, the specimen shows a long, horizontal, leafless branch, which consists of several stretched internodes, and with a pair of flowering stems (F) developed at each node, in the axils of the leaves, which have now faded away. This long, horizontal branch represents a vegetative shoot (V*) in its second year, and when the axillary shoots (F) have reached maturity and developed roots, the old internodes die off, and a series of independent individuals is produced. These vegetative shoots being above ground, and no subterranean stolons being developed, our plant may be well characterized as being perennial, but without a rhizome. However, the base of the floral shoot does not die off with the aerial portions, but stays alive and produces axillary buds, which, later on, develop into aerial stems; such perennial stem-bases are called pseudo-rhizomes. It is thus characteristic of this species of *Stellaria*, that some of the aerial shoots remain vegetative: that they become horizontal, and develop new, axillary shoots, which soon become separated from the mother-plant as independent individuals. These vegetative shoots thus become developed as stolons above ground. We find this same method of reproduction in *Phlox divaricata* L. with the only exception that the stolons persist here for several years and continue their growth, developing axillary shoots without becoming separated from the mother-plant. In *Phlox reptans* Michx., on the other hand, the stolons become terminated by an inflorescence preceded by a rosette of leaves in the same manner as in *Antennaria*. But in regard to the *Caryophyllaceæ* we have only observed this type of reproduction in *Stellaria pubera*.

In the second type we have plants which persist by means of hibernating buds above ground and by subterranean stolons; as an example of this method of reproduction may be mentioned:

Stellaria longipes Goldie.

Common on the arctic shores, and not infrequent in the alpine region of the Rocky Mountains,* this little herb shows a remarkable power to withstand the severity of the winter; it has been described by Kjellman in his interesting paper on

* Collected by the writer on several peaks in Colorado at an elevation of 12,000 to 12,500 feet.

the life of the polar-plants.* In this species the rhizome consists of long stolons with small scale-like leaves, and stretched internodes. The aerial shoots are ascending, and the leaves are more or less crowded on account of the shortness of the internodes. When the winter commences the leaves are still attached to the shoots, but in a withered condition; the stems, on the other hand, remain alive and persist throughout the winter. At the beginning of the spring small buds become visible in the axils of the withered leaves, which soon develop into small leafy shoots. These shoots frequently remain vegetative for one or two years until they become terminated by an inflorescence. We have, thus, in this species of *Stellaria* a very interesting example of herbaceous aerial stems, which winter over, and produce axillary buds, the function of which is to develop assimilating leaves, new axillary buds, and finally to produce flowers and fruits. This method of reproduction we observed, also, in the alpine plant, but in this the axillary shoots frequently reach the flowering stage already in the first year of their growth.

Several other species of *Stellaria* exhibit this type of vegetative reproduction, for instance: *S. longifolia* Muehl., *S. humifusa* Rottb., *S. Holostea* L.,† and *S. crassifolia* Ehrh. But in *S. borealis* Big. (specimens from Hudson Bay, and St. Paul island in Behring Sea), and in *S. crispa* Cham. et Schl. (from Annette island, Alaska) we observed only the subterranean stolons; thus it appears as if the aerial stems of these two species do not persist throughout the winter.

As representing this type may, furthermore, be mentioned

Stellaria umbellata Turcz.

This species we collected in Colorado on the summit of the mountains (above 14,000 ft.), where it grows among bowlders, associated with *Claytonia megarhiza*, *Trifolium manum*, *Saxifraga cernua*, *S. flagellaris*, *S. nivalis*, *Poa Lettermannii*, etc.; it occurs, also, at lower elevations, for instance in the Spruce-zone on Mt. Massive (10,500 ft.).—In the alpine plant the aerial shoots (fig. 2) are very short with crowded leaves and a small, terminal inflorescence, mostly three-flowered; the stems persist throughout the winter, and minute buds become formed in the axils of the withered leaves as in *S. longipes*. There is a very distinct rhizome, consisting of several stolons, in which the internodes are very short, and mostly shorter than the

* Ur Polarväxternas liv (in A. E. Nordenskiöld's Studier och Forskningar, Stockholm. p. 513, 1884).

† An interesting account of the hibernation of this species has been given by O. G. Petersen (Bot. Tidsskr., ser. 2. vol. 4. Kjøbenhavn, 1874-76, p. 30), who has, also, described the development of cork as it occurs in *Caryophyllaceae*, and the structure of the pericycle (ibidem, p. 187, 1888).

small, fleshy, scale-like leaves (fig. 3). In specimens from lower altitudes the stems are taller, and the inflorescence is an amply ramified cyme, beside that the stolons are much longer with the internodes stretched, almost to the same extent as in the species described above.

The internal structure of the alpine plant is quite characteristic; the green leaves have a larger number of stomata on the ventral face than on the dorsal, and these are surrounded by four or five ordinary epidermis-cells; they are level with epidermis, and the air-chamber is wide, but shallow. In most of the other *Caryophyllaceæ* the stomata are surrounded by two subsidiary cells, which are arranged vertical on the stoma.* The chlorenchyma consists of a typical palisade-tissue of one or two layers, and an open pneumatic tissue below this. There is a small, thinwalled water-storage tissue on the leptome-side of the midvein, but in regard to the mechanical tissues we find only a very few, thinwalled stereome-cells on the dorsal face of the midvein, but inside the parenchyma-sheath. The leaves of the stolons have, of course, no stomata, and the chlorenchyma represents a homogeneous tissue of roundish cells filled with starch, and very compact; the veins are, also, here surrounded by thinwalled parenchyma-sheaths, and lack mechanical support.

The aerial stem has a thickwalled epidermis with prominent, longitudinal ridges on the outer cell-wall, covered by a thick, smooth cuticle; the cortex is quite compact, and a thinwalled endodermis surrounds a pericycle of slightly thickwalled stereome. The stele consists of an almost continuous zone of leptome and hadrome, with a central pith of moderately thickwalled cells. A corresponding structure is to be observed in the subterranean axes, the stolons, but the pericycle is here very thinwalled, and the stele is composed of four separate mestome-strands and a broad, central pith.

This peculiar method of hibernation is thus characteristic of species that occur under very extreme climatologic conditions: in the far north, and on the summit of high mountains. We now pass to describe the third type of vegetative reproduction, in which a strongly developed rhizome occurs, and in which the aerial stems are strictly annual. This type is represented by

Stellaria Jamesii Torr.

This species is an inhabitant of the wooded belts of the Rocky Mountains in Colorado. The slender stem is terminated by a large, leafy cyme, and the lower stem-leaves subtend short, vegetative branches, which do not winter over; the aerial stems,

* Compare Solereder: Systematische Anatomie der Dicotyledonen. Stuttgart, p. 122, 1899.

thus, die down to the ground at the end of the first season. As mentioned above, this species possesses a rhizome which shows a much higher development than that of other American representatives of the genus. Our figures 4-6 illustrate the external structure of the rhizome. It is horizontally creeping; the internodes are partly swollen and tuberous; they root freely, especially at the nodes. The leaves of the rhizome are opposite, scale-like, and membranaceous; they support buds, of which those that are located near the apex of the rhizome develop into aerial, floral shoots; the others stay dormant. It is a structure which is very common, and characteristic of many, very different genera, but it seems to be very rare within the *Alsineæ*, and perhaps within the *Caryophyllaceæ* in general. If we examine the internal structure, we notice the same structural peculiarities which we are used to find in rhizomes that store nutritive matters. In the slender portions of the internodes the epidermis is thinwalled, and no hypoderm is developed; the cortical parenchyma consists of about five layers, and does not contain starch; a few layers of very thinwalled cork, which has originated from the innermost stratum of the cortex, surround a pericycle of a closed sheath of mostly six layers of moderately thickened collenchymatic tissue; but there is no endodermis. We find in the stele five separate, collateral mestome-strands, which contain cambium. There is no interfascicular cambium; thus the mestome-strands are located in the periphery of a broad central parenchyma, which contains druids of calcium oxalate, and large deposits of starch, the starch-grains being of equal size, and quite large.

A corresponding structure is to be observed in the swollen portion of the internodes, with the exception of the pith being much broader, and the mestome-strands, the secondary, having a much longer radius, when viewed in cross-sections. The structure of the primordial mestome is as described above, but the secondary hadrome appears here as a long and very narrow line of vessels in each strand; the pith is hollow in the center. The secondary formations are, thus, limited to the stele, and the nutritive matters are deposited in the pith, but not in the cortex.

In bringing these facts together it is readily to be seen, that our species of *Stellaria* are not so very uniformly developed in regard to the means by which the hibernation and vegetative reproduction is effected. The three biological types which we have suggested are well marked, and might, with some benefit, be included in the specific diagnoses. But otherwise the morphological structure is very uniform in this genus, and we might at the same time take the opportunity to make a correction in regard to the inflorescence, as described in the Synop-

tical Flora (l. c., p. 233-236). The inflorescence is constantly terminal in *Stellaria* as in all the other members of the family, but it happens, sometimes, that the flowers become overtopped by the excessive growth of an axillary, vegetative shoot. This is, for instance, the case with *S. longifolia*, which is said to have a "lateral cyme." In *S. crispa* the flowers are not "solitary, axillary," but terminal. However the ramification of this species is quite singular, and it may look as if the flowers were axillary, but only apparently so. The shoots are very long, and leafy to the top; not infrequently the single flower is placed next to a long shoot with many pairs of leaves, and also bearing a single flower, accompanied by a long vegetative shoot. The flower is terminal, however, but instead of occupying the center in a cyme, it is single, since only one lateral shoot becomes developed from the uppermost pair of opposite leaves, and this shoot being frequently vegetative in its entire length. It is far from seldom, however, to find specimens which show the normal structure in a perfectly typical manner. Among the specimens which Mr. Kearney collected in Alaska and kindly placed at our disposal, there are some in which the shoots are terminated by a single flower, and in which no axillary, vegetative branch has been produced; in others the terminal flower is located between two very short branches, each of which is again terminated by a flower.

Brookland, D. C., December, 1907.

EXPLANATION OF FIGURES.

FIG. 1. *Stellaria pubera* Michx. showing a vegetative shoot (V) in its first year of growth, and another (V*) in its second year; the shoots marked F are floral; one half natural size.

FIG. 2. A complete specimen of *S. umbellata* Turcz. from an elevation of 14,200 feet (Colorado); stolons with scale-like leaves are developed from the subterranean stem-portion; natural size.

FIG. 3. Two stolons of the same species; 2 × natural size.

FIGS. 4, 5, 6. Tuberos rhizomes of *S. Jamesii* Torr.; one half natural size.