ART III.—*Chionophila* Benth. *A Morphological Study*;
by THEO. HOLM. (With 15 figures, drawn from nature
by the author.)

The genus *Chionophila* Benth. is a member of the tribe Cheloneae, and its nearest allies in North America are *Chelone* and *Pentstemon*; as distinguishing characters Gray, Bentham and Hooker consider the structure of the calyx, corolla and fruit as the most important. The calyx being funnelform, obtusely five-lobed in *Chionophila*, deeply five-parted in the two other genera; the corolla being densely bearded at the base of the lower lip in *Chionophila*, while in *Pentstemon* this structure recurs only in certain species: *P. barbatus* Nutt., *P. laevigatus* Soland., *P. pubescens* Soland., and a few others; moreover the capsule being septicidally dehiscent in *Chelone* and *Pentstemon*, but at first loculicidal in *Chionophila*; in the last of these the capsule is enclosed in the marcescent calyx and corolla, while it is free in the others; also the seeds are different, being rather large, oblong, with a very loose, reticulated outer coat in *Chionophila*, winged in *Chelone*, and angulated, but marginless in *Pentstemon*. Very little, however, is said about the habit of *Chionophila*: *Herba perennis, humilis, caespitosa, glabra* is the characterization offered by Bentham and Hooker; a dwarf perennial, glabrous or nearly so is all, that Gray has to say.

At the time of Bentham and Gray the genus was supposed to be monotypic, but since then a second species has been proposed by Professor L. F. Henderson¹ *C. Tweedyi*, by Canby and Rose referred to *Pentstemon*, *P. Tweedyi*. However this second species differs from *C. Jamesii* Benth. according to Professor Henderson, by the corolla being quite saccate at base dorsally, thus causing the corolla to be turned aside at quite a strong angle with the axis of the inflorescence, beside by the calyx being short and more lobed, and the lower lip of the corolla being merely papillose. Professor Henderson found this new species in open, loose soil at the bases of mountains in Idaho. *C. Jamesii*, on the other hand, is a member of the high alpine flora of the Rocky Mountains of Colorado and Wyoming.

¹ Henderson, L. F. New Plants from Idaho and from other localities of the North West. (Bull. Torr. Bot. Club, vol. 27, 1900, p. 352.)

² Canby and Rose in Bot. Gazette, vol. 15, 1896, p. 67.

Recently *C. Tweedyi* has been raised to generic rank, receiving the unfortunate name "*Pentstemoniopsis*,"³ for as will be shown in the subsequent pages, the plant is undoubtedly just as close an ally of *Chionophila* as of *Pentstemon*; moreover the frequent use of making generic names by adding "*opsis*" has resulted in names of too great length, and sometimes also in such terrific combinations as: *Saxifragopsis*, *Stellariopsis*, *Bombacopsis* etc.

Now with respect to *Chionophila Jamesii* the plant is not caespitose, but stoloniferous, and the shoot above ground shows very plainly the structure of a typical monopodium. There is a rosette of leaves, and generally only one flower-bearing stem, which is axillary. In the center of the rosette is a bud, vegetative, which terminates the shoot, and the flower-bearing stem is always axillary, proceeding from near the base of the shoot, from the axil of one of the basal leaves. The leaves are opposite with long sheaths, and the accompanying diagram (fig. 1) shows the structure, which is the commonest met with. Four pairs of leaves constitute the rosette, *L*.¹—*L*.⁴; of these *L*.⁴ enclose a vegetative bud, which will develop a new rosette in the coming year, and in the axil of one of the leaves *L*.¹ is a floral stem (*St.*) When stolons develop, they generally proceed from the axils of the leaves of the previous year, now present as withered leaf-sheaths, and these stolons consist of two to three stretched internodes, covered by leaf-sheaths; they grow in a horizontal direction, and become terminated by a rosette of leaves, repeating the structure of the mother-shoot. During the first season the stolons remain attached to the mother-shoot, and roots develop freely from the nodes. The number of stolons may vary from one to as many as six, but one or two are the most frequent. The subterranean stem is ascending, densely covered with remnants of leaf-sheaths, and of a soft, fleshy consistence.—The monopodium represents a structure, which is evidently rare; we remember this structure being characteristic of certain species of *Carex*, for instance *C. laxiflora*, *C. digitata*, *C. Fraseri* and some others, which I have described in this journal. A sympodium, however, is the most frequent structure observed in rhizomes especially. Among the Smilacaceae *Smilax herbacea* shows the interesting case of

³ Rydberg, P. A. Flora of the Rocky Mountains, New York 1917.

the rhizome representing a sympodium, while the aerial stem is a true monopodium. Unfortunately the literature gives little information about these structures, and with regard to the structure of the shoot above ground being a monopodium so distinctly represented by *Chionophila*, there is no mention of this structure being represented by any of the other Scrophulariaceae; as a matter of fact the word "monopodium" does not occur in any of the American manuals of Botany, dealing with floras of certain regions. Nevertheless it constitutes a character of no small importance, and none of the species of *Pentstemon*, which I have examined, exhibit this structure. It may be mentioned at the same time, that *Arabis dentata* exhibits a monopodium exactly as that of *Chionophila*, and is the only *Arabis*, known so far, of which the shoot is of monopodial growth. The monopodium occurs also in *Claytonia*, *Calandrinia*, *Viola* etc., which I have described in previously published papers on these genera.

Concerning the inflorescence in *Chionophila*, this is not a spike, but a unilateral cyme, a monochasium; the floral stem begins with two or three pairs of small, linear, opposite bracts without buds; but above these the bracts become somewhat larger, broader, and we find at each pair a single flower, and a lateral branch, which again terminates in a flower with two bracts and a lateral branch and so on. In *Chionophila* the composition of the inflorescence is not so very distinct on account of the short internodes, the leaves and flowers being rather crowded, but in *Collinsia grandiflora* Dougl. the structure is plainly visible, and corresponds exactly with that of *Chionophila*. In *Pentstemon*, on the other hand, there is a regular cyme in the axil of each leaf; in *P. Newberryi* Gr. the axillary cymes are one-flowered, there being only a single flower, but with two bracts, indicating a "dichasium" with two lateral branches suppressed, non-developed.

Characteristic of *Chionophila*, when compared with *Pentstemon*, is thus the monopodial ramification of the shoot, and the inflorescence representing a monochasium. The floral structure has been described very exactly by Gray, Bentham and Hooker, except that it seems to have been overlooked, that the calyx, in fresh specimens, is distinctly folded lengthwise as shown in figure 2.

Internal structure of the vegetative organs.

The roots:—In Solereder's treatment of the Scrophu-

lariaceae nothing is said about the root-structure. With respect to *C. Jamesii* the structure is of special interest, since I observed the development of cork to take place in the peripheral stratum of the cortex, the stratum bordering on the exodermis (fig. 5), and, as we remember, De Bary records only two cases of cork being developed in the peripheral strata of the root-cortex, namely in *Clusia* and *Bignonia capreolata*;⁴ since then Olivier detected a similar structure in *Artanthe pothifolia*, *Jasminum humile*, and *Ruyschia Souroubea*;⁵ to these may be added *Tecoma radicans* and *Cephalanthus occidentalis*.⁶

There was no primary root in any of the specimens, which I collected, and the root-system consisted merely of several strong, secondary roots developed from the subterranean part of the stem; these roots were sparingly branched, and only slightly hairy. Inside the epidermis is a thinwalled, contractile exodermis (Ex. in fig. 5), covering an open cortical parenchyma of about twenty layers, with no starch or crystals; a phellogen (Ph.) arises, as stated above, in the peripheral stratum. Inside the cortex follows a thinwalled endodermis (End. in figure 6), surrounding the pericambium (P), in which tangential cell-divisions appear outside the protohadrome, being the only indication of secondary increase in the young roots. The roots are pentarch with five strands of leptome alternating with five short rays of hadrome. The center of the stele represents a relatively broad, thinwalled pith without starch.

As the roots grow older the cortex collapses, and some few secondary vessels develop on the inner flank of the leptome. The main stem, which is terminated by the rosette of leaves, shows the following structure. The upper internodes are cylindric, glabrous and smooth. A thin cuticle covers the slightly papillose epidermis, and the cortical parenchyma is homogeneous, of about twenty strata with distinct intercellular spaces, and containing a little starch. There is no endodermis, and no pericycle, but a band of isolated, small strands of leptome, and a continuous band of cambium, inter- as well as intra-fascicu-

⁴ De Bary, A. *Vergleichende Anatomie*, p. 563. 1877. See also Van Tieghem, Ph. *Recherches sur la symétrie de structure des plantes vasculaires*. (Ann. sc. nat. Bot. Ser. V, 13. p. 258. 1870.)

⁵ Olivier. *Recherches sur l'appareil tégumentaire des racines*, *ibid.* Ser VI, 11. p. 124. 1880.

⁶ Holm, Theo. *Rubiaceae*; *Bot. Gaz.*, (vol. 43, p. 155). 1907.

lar; there are eight primary mestome-strands with a few vessels, but with neither mestome-parenchyma nor libriform; the center of the stele contains a thinwalled, starch-bearing pith. Further down, and below the rosette, the epidermis is more or less collapsed, and replaced by two to three layers of cork, developed from the hypodermal structure of the cortex. The cortex is as above; in the stele is no endodermis, but a parenchymatic pericycle, and two concentric bands of leptome, separated by some ten layers of radially arranged parenchyma, a secondary cortex. Some secondary vessels may be seen in the primary mestome-strands, and the hadrome thus constitutes much deeper rays than in the internodes above.

The flower-bearing stem, which is axillary, is two-winged at the base, with the stele circular (in cross section). It is glabrous and smooth, but the cuticle is, here and there, wrinkled longitudinally. The epidermis is thickwalled, especially the outer cell-wall, and the cortex is also somewhat thickened, and consists of six to seven strata, very open from the wide intercellular spaces, and destitute of starch and crystals. Endodermis is barely distinct (End. in fig. 7), and the pericycle is merely present as a single layer of small-celled parenchyma (P. in fig. 7), which is continuous and bordering directly on the numerous small strands of leptome. There are eight primary mestome-strands, containing a few (four) layers of radially arranged, thickwalled, and porous mestome-parenchyma. The interfascicular tissue consists of leptome, and three to four layers of radially arranged, thickwalled parenchyma. The pith is solid, homogeneous, with no starch or crystals (fig. 7). In the wings of the stem is only thinwalled cortex, no collenchyma being developed.

This portion of the flower-bearing stem was subterranean, but the structure of the upper, aerial internodes is about the same. However, small hairs with cuticular pearls (fig. 9) occur on the internodes, and the cuticle is more wrinkled. The epidermis is more thickwalled, the cortex contains chlorophyll, and is very open from lacunae of quite considerable width, but otherwise the inner tissues are as described above.

Characteristic of the stem is thus the complete absence of collenchyma and stereome, the only strengthening tissue being represented by the thickwalled, interfascicular parenchyma.

The leaf.—The leaves of the rosette are thick, fleshy, and glabrous; they are held in an almost vertical position,

and the stomata are equally distributed over both faces of the blades. While cuticular striations are very pronounced on the ventral face of the leaf, (fig. 10) the cuticle

is smooth on the dorsal. Viewed "en face" the lateral cell-walls of epidermis are, on both faces, straight, quite thick and porous, especially on the dorsal face; the stomata (fig. 8) are free, and surrounded by mostly four ordinary epidermis-cells. In cross-sections the structure of the cuticle is readily visible (fig. 10), and the outer cell-wall of epidermis appears quite thick. The chlorenchyma consists of four layers of palisade-cells, which cover a very open pneumatic tissue of about eight strata. In the marginal portion of the leaf the palisade-tissue extends to the dorsal part of the blade and there is no mechanical tissue neither stereome nor collenchyma in any part of the leaf. The mestome-strands are collateral, all single, and surrounded by green parenchyma sheaths. The leaf-structure is thus approximately isolateral on account of the distribution of the stomata, but not with reference to the structure of the chlorenchyma. The leaf-structure thus resembles that of the high alpine *Claytonia megarrhiza*,⁷ as far as concerns the distribution of the stomata on both faces of the blade, the several strata of palisade-cells, the thick cuticle and thickwalled epidermis. Bonnier⁸ and Wagner⁹ have offered some interesting contributions to the knowledge of the structure of alpine plants, and according to these authors the leaf-structure of *Chionophila* and of *Claytonia megarrhiza* appears to be the typical one, which characterizes the overwintering leaves of alpine species. And the highly developed assimilating tissue is in correlation with the pronounced intensity of light at the higher elevations, the considerable decrease of carbonic acid in the atmosphere, beside the very short time of vegetation. At the same time these winter-green leaves are protected against too excessive transpiration during the period of the melting of the snow, by means of the very thick cuticle and pronounced thickening of the cell-walls of epidermis. However, only the leaf has been studied by these authors and the Monocotyledones have,

⁷ Holm, Theo. *Claytonia Gronov*, Mem. Natl. Acad. of Sc., vol. 10, Washington.

⁸ Bonnier, G. Cultures expérimentales dans les hautes altitudes, (Comptes Rend. Acad. Sc., 1890).

Bonnier, G. Influence des hautes altitudes sur les fonctions des végétaux, (ibid. 1890).

Bonnier, G. Etude expérimentale sur l'influence du climat alpin sur la végétation et les fonctions des plantes, (Bull. Soc. Bot. de France, 1888).

⁹ Wagner, A. Zur Kenntniss des Blattbaues der Alpenflanzen und dessen biologischer Bedeutung. (Sitzungsber. Akad. Wiss. Wien, Math. nat. classe, May, 1892).

almost, been passed by in silence. To obtain a more complete idea of the alpine structure and its correlation with the surrounding medium it will be necessary to include the stem as well as the root structure, and to decide whether certain structural peculiarities may be really epharmonic or inherited.

Finally with reference to *Pentstemoniopsis* this plant shows exactly the same monopodial growth as *Chionophila*: a terminal rosette of leaves, axillary floral stems, and axillary stolons. The monochasium is also represented in this plant, and more distinctly than in *Chionophila*, since the inflorescence is more open. The seeds also agree with those of *Chionophila* (fig. 15), but the flower and the fruit resemble those of *Pentstemon*. The habit of the plant thus corresponds with that of *Chionophila*, the deeply cleft calyx and the free capsule with those of *Pentstemon*. The corolla with the lower lip bearing short-papillae instead of distinct hairs as in *Chionophila* is of small importance, but the gibbous base, and the horizontal position of the flower render the plant distinct from both, and especially when combined with the monochasial ramification of the inflorescence.

Pentstemoniopsis is undoubtedly a good genus, if we include the vegetative characters, and the structure of the inflorescence in the diagnosis.

EXPLANATION OF FIGURES.

FIG. 1. *Chionophila Jamesii*. Diagram of the shoot; for explanation see the text.

FIG. 2. The flower, seen from above; enlarged.

FIG. 3. The fruit surrounded by the marcescent calyx and corolla; enlarged.

FIG. 4. The capsule removed from the calyx and corolla; enlarged.

FIG. 5. Cross-section of a secondary root; Ep.=epidermis; Ex.=exodermis; Ph.=phellogen; X 320.

FIG. 6. Cross-section of inner part of same root; C.=cortex; End.=endodermis; P.=pericycle; L.=leptome; V.=vessels; X 496.

FIG. 7. Cross-section of inner part of stem; S.=pericycle; P.=pith; H.=hadrome; other letters as above; X 320.

FIG. 8. Ventral epidermis of leaf with a stoma; X 496.

FIG. 9. Epidermis of stem with hairs; X 320.

FIG. 10. Dorsal epidermis of leaf; X 496.

FIG. 11. *Pentstemoniopsis Tweedyi* (Rose) Rydbg. The flower, side-view; enlarged.

FIG. 12. Lower lip of flower; enlarged.

FIG. 13. The stamens, four fertile, one sterile; enlarged.

FIG. 14. The fruit; enlarged.

FIG. 15. The seed; enlarged.

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