Bartonia, Muehl. An Anatomical Study.

BY

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With Plates XXXIII and XXXIV.

IN systematic works dealing with Gentianeae, *Bartonia* and *Obolaria* are invariably placed side by side on account of the following characters: 'Lobes of the corolla imbricated in the bud, i.e. two exterior and two interior; no appendages; ovules and extremely numerous, minute, close-coated seeds covering the whole parietes of the ovary and capsule; stamens inserted in or little below the sinuses of the corolla; anthers ovate-sagittate; foliage hardly any or discoloured' (Gray: Synoptical Flora of North America). Or 'corolla efoveolata, lobis imbricatis' (Bentham et Hooker). A like characterization is offered by Gilg (Natürl. Pflanzenfam. iv, 2), but with the additional remark: 'Schwachgrüne Halbsaprophyten.' By Bentham, Hooker, and Baillon these genera are placed among the Swertiaeae, by Gilg among the Erythraeinae.

In regard to *Obolaria* the writer has, some years ago, described some of the most salient points in its external and internal structure¹, and we have shown that the corolla does possess nectaries in the shape of small, fringed scales, besides that the plant contains chlorophyll in abundance, and that the coralloid roots represent mycorrhizae. In habitus the genus differs very much from *Bartonia*; it is a rather robust plant in proportion to its size, and the fleshy leaves are very conspicuous. In *Bartonia*, on the other hand, we meet with plants of exceedingly slender habit, threadlike stems and minute, subulate leaves. Common to both is the presence of chlorophyll and coralloid mycorrhizae.

When Gray (l. c.) described *Bartonia* only two species were known: *B. verna*, Muehl. and *B. tenella*, Muehl., the latter with a variety *Moseri*. Since then two more species have been established, viz. *B. lanceolata*, Small², and *B. iodandra*, Robins³. Characteristic of the latter is the colour of the anthers, being sometimes purplish or dark maroon, besides the calyx being

¹ Annals of Botany, vol. xi, no. xliii, September, 1897, p. 369.

² Flora of the South-eastern United States, 1903, p. 932.

³ Botan. Gazette, 1898, p. 47, and Rhodora, vol. ii, p. 56.

turbinate below. The former, *B. lanceolata*, is characterized by possessing lanceolate corolla-lobes, which are entire, acute or acuminate, in contrast to *B. tenella* in which the corolla-lobes are oblong and erose; but the differences in the structure of the stigma are not mentioned. In regard to the geographical distribution of these species, *B. verna* occurs in the southern States from S. Virginia to Florida and Louisiana; *B. tenella* and *B. lanceolata* are widely dispersed in the Atlantic States from Connecticut to Florida, west to Wisconsin and Arkansas; while *B. iodandra* is a more northern plant, having been found only in Newfoundland, Nova Scotia, and Massachusetts. In the District of Columbia and Maryland *B. lanceolata* is the only species that has been observed by the writer. It would thus appear as if *B. verna* and *B. iodandra* occupy a more distinct geographical area than the others, even if these have not, so far, been found directly associated with each other.

In regard to the specific merits of these four plants, *B. verna* is perhaps the most constant and the most readily distinguished. Besides being vernal (the three others are autumnal), the pure white corolla and the compressed ovary make it very distinct. The lobes of the corolla are spreading (Plate XXXIII, Fig. 1), one-nerved, obtuse and very minutely erose (Fig. 2); the stigmatic surface (Fig. 4) of the ovary is long and very prominent. In *B. lanceolata* the corolla-lobes are erect (Fig. 9), lanceolate, more or less involute along the margins, and three-nerved (Fig. 7), besides that the colour is yellowish to white; the ovary of this species (Fig. 10) is quadrangular in cross-action, and the stigmatic surface very small, not extending beyond the corolla (Fig. 9). In *B. tenella*, on the other hand, the lobes of the corolla (Fig. 18) are oblong, obtuse, erose and three-nerved, and the colour is frequently more or less purplish; the stigmatic surface (Fig. 19) is very conspicuous and raised above the corolla (Fig. 17). Intermediate between *B. lanceolata* and *B. tenella* is the little-known *B. iodandra*, in which the flesh-coloured corolla-lobes are broadly oblong and obtuse, while the stigmatic surface is small and does not reach beyond the corolla. The flowers are usually somewhat larger than those of *B. tenella*, and the calyx is, as already stated, turbinate below. It may be that *B. iodandra* represents a mere geographical form of *B. tenella*.

The inflorescence is a cyme in all the species, but often somewhat irregular on account of the leaves being, sometimes, not exactly opposite, and this is especially the case with *B. iodandra*, besides in weak, few-flowered specimens of *B. lanceolata* (Fig. 5). Small, one-flowered specimens of *B. verna* are common, while the largest number of flowers observed in this species is nine; but three-flowered individuals appear to be the most frequent. In *B. tenella* and *B. lanceolata* (Fig. 6) the inflorescence is often ample and rich-flowered.

Characteristic of these species are the minute, appressed leaves, normally

opposite, but very frequently not so; in vigorous specimens of *B. tenella* and *B. lanceolata* they are often quite crowded and strictly opposite at the base of the stem. The root-system is poorly developed and only represented by some few slender, secondary roots, there being no primary. The germination seems to be unknown.

In regard to the internal structure our genus is very little known, and no mention has been made in Dr. Solereder's comprehensive work on the Anatomy of Dicotyledons¹. Nevertheless the structure has been touched upon, though very briefly, by W. Bötticher² and E. Perrot³ in their treatments of the Gentianaceae. These plants are, as a matter of fact, very difficult to study from dried and pressed material alone, and since the writer has been able to obtain fresh specimens of *B. verna* and *B. lanceolata*, we take the opportunity to present the following results of our anatomical investigation, concerning the vegetative organs.

BARTONIA VERNA, Muehl.

The Roots.

As stated above, the roots are mycorrhizae; they are somewhat fleshy, sparingly branched, and lack hairs; they are not contractile. A thin-walled epidermis covers directly the cortical parenchyma, no exodermis being developed. The cortex consists of about six compact layers, in which fungal hyphae are very frequent. Endodermis is thin-walled, and shows the Casparyan spots very plainly. The thin-walled, continuous pericambium surrounds two groups of leptome, alternating with two rays of hadrome, and the narrow vessels extend to the centre of the root. Other roots were observed to be triarchic.

The Stem.

The basal internode is cylindric, glabrous and smooth. A thick, wrinkled cuticle covers the epidermis (Plate XXXIII, Fig. 11), of which the external and radial cell-walls show a very pronounced thickening; some stomata were observed (Fig. 11), and they were level with the surrounding epidermis. Inside the epidermis is a cortical parenchyma of about nine layers of thin-walled cells with narrow but distinct intercellular spaces. The cells of the cortex contain a little chlorophyll and are of about the same size throughout, but only the innermost strata are arranged radially, although no endodermis was observed. The cortex borders thus directly on the mestome-strands, the structure of which is very irregular, there being about ten groups of leptome, but an almost continuous ring of hadrome, besides four leptomatic strands, located in the pith. The innermost

¹ Systematische Anatomie der Dicotyledonen, 1899.

² Beiträge zur vergleichenden Anatomie der Gentianaceen. Inaug. diss. Erlangen, 1895, p. 55.

³ Anatomie comparée des Gentianacées. Thesis. Paris, 1899, p. 192.

portion of the stem is occupied by a thin-walled but compact pith with no deposits of starch.

If we examine one of the internodes from the middle of the stem, the structure is somewhat different. The cross-section is quadrangular, and stomata are more frequent (Plate XXXIV, Fig. 23); they are surrounded by four cells. A typical, thin-walled endodermis is differentiated in this part of the stem, but otherwise the structure of the cortex and epidermis is identical with that of the basal internode. The mestome-bundles are very irregular (Plate XXXIV, Fig. 20), some being bicollateral, others being reduced to a small group of vessels, bordering directly on the endodermis (Fig. 24), and the hadrome does not here form a closed ring around the pith. We noticed six groups of leptome in the pith, and these were more or less separated from the hadrome, as may be seen in our figure (24).

In the apical internodes we notice the same structure and the same irregular development of the mestome-bundles. For instance, as shown in Fig. 12, pure leptomatic strands occur within the endodermis, or the mestome-bundles may be strictly collateral, though exceedingly small, as figured on Plate XXXIII, Fig. 13.

It thus seems characteristic of this species that the stem lacks mechanical tissues, stereome and collenchyma, and that epidermis is the only tissue that has acquired some strength and firmness by the thickening of the cell-walls.

The Leaf.

All the leaves of *Bartonia verna* are minute, subulate and appressed to the stem; they are triangular in cross-sections with a keel on the dorsal face. The cuticle is thick, wrinkled on both faces of the blade. Viewed *en face*, the cells of epidermis are rectangular with the radial walls slightly undulate; in transverse sections the cells on the dorsal face are conspicuously larger than on the ventral; the outer cell-wall is moderately thickened on both faces. Stomata surrounded by four cells were observed on both faces, but they are most frequent on the dorsal. The chlorenchyma represents a homogeneous tissue of roundish cells loosely connected, and often traversed by a lacune near the centre; chlorophyll, but only in small quantity, was observed. There is only one vein, located in the keel; it consists of a small mestome-strand, destitute of mechanical support, and has no parenchyma-sheath either. The elements of the leptome are very small, and the hadrome contains only a few, narrow vessels.

Glandular hairs of the same structure as those which we observed in *Obolaria* (l. c.) were noticed at the very base of the leaves, but only on the ventral face.

BARTONIA LANCEOLATA, Small.

The Roots.

The roots are short and slender, sparingly branched and of a brownish colour; no hairs were observed. Hyphae were found in epidermis, exodermis, and in all the cells of the cortex. Inside epidermis is a single layer of thick-walled cells representing an exodermis. The cortex consists of three strata of large, roundish cells with wide intercellular spaces. It borders on an endodermis, the cells of which are thin-walled and much smaller than those of the cortex proper; the Casparyan spots were plainly visible. A thin-walled, continuous pericambium surrounds three small strands of leptome alternating with three rays of hadrome, the vessels of which are very narrow. Some other roots that were still thinner contained only two leptome-strands and two hadromatic rays.

Although the majority of roots examined proved to be mycorrhizae, we did observe a few in which no hyphae were to be traced. The structure of these roots agreed, however, with that of the others, but the epidermis showed here a tendency to develop low papillae, the exodermis was quite thin-walled, and the tissues showed a more regular structure and arrangement than observed in the mycorrhizae.

The Stem.

One of the basal, cylindric internodes shows the structure as follows: A wrinkled cuticle covers the epidermis, the outer cell-walls of which are moderately thickened; no stomata were observed, the internode being underground. No exodermis is differentiated, thus the cortex borders directly on epidermis; the cortical parenchyma consists of seven layers in which the intercellular spaces are quite wide; no chlorophyll or starch was noticed. There is, furthermore, an endodermis (Fig. 22), mostly thin-walled, or some of the cells showed a thickening all around, but only outside the leptome. A continuous ring of thick-walled cells separates the leptomatic strands from the hadrome, thus forming a protective sheath around the hadromatic cylinder. The cells of this sheath are, in longitudinal sections, longer than those of endodermis, and their cross-walls are straight and horizontal; they are of a lighter colour than the vessels, and the walls are porous. Morphologically the elements of this protective sheath may be defined as representing thick-walled mestome-parenchyma rather than modified sclerenchyma. In regard to the leptome this tissue occurs as isolated strands, about ten in all, bordering directly on endodermis. The hadrome, on the other hand, forms a closed cylinder of vessels in several layers, wide reticulated and narrower scalariform. The central portion of the internode is occupied by a solid but thin-walled pith, in which no

deposits of starch were observed. In this pith are located about eight leptome-strands, which are not arranged so as to correspond radially with the peripheral leptome, and they all are separated from the hadrome by layers of parenchyma pertaining to the pith.

A somewhat different structure is to be observed in the lowermost of the aerial internodes, a short distance above the one described in the preceding. The internode is obtusely quadrangular in cross-section, and stomata occur; these are level with epidermis and surrounded by four cells (Fig. 21). The cortical parenchyma is here composed of only three strata, which contain chlorophyll, and the intercellular spaces are very wide. Endodermis is very thick-walled and porous, and surrounds a central cylinder of the same constituents as described above, and arranged in the same way. The mestome-parenchyma is, however, more thick-walled than observed in the subterranean internodes, and the mestome represents now about eight distinct bicollateral mestome-strands, instead of a confluent mass of hadrome and isolated leptome, the innermost groups of which border here almost directly on the hadrome. The pith shows the same structure as above, but extends now between the hadrome to the protective sheath.

This same structure was observed in all the other internodes above, but the cross-section becomes gradually more sharply quadrangular, and at the same time the number of peripheral leptome-strands becomes reduced to only four outside the several groups of hadrome with leptome on the inner side.

In the peduncles of the flowers we noticed a corresponding structure, and chlorophyll was observed in the guard-cells of the stomata and in the cortex. The peduncle is sharply quadrangular, and contains a thin-walled endodermis, surrounding a central cylinder with four broad strands of leptome corresponding with the four angles, besides a sheath of thick-walled mestome-parenchyma as above. The hadrome forms an almost closed ring with about five internal strands of leptome, and a central, thin-walled pith without starch.

The Leaf.

The leaves are of the same shape and small size as those of *B. verna*, and possess the same kind of glandular hairs as observed in this species. A transverse section of the leaf (Plate XXXIII, Fig. 16) shows a smooth cuticle and a moderate thickening of the outer cell-walls of epidermis. Stomata level with epidermis occur on both faces of the blade. The chlorenchyma constitutes a homogeneous tissue of roundish cells, which contain chlorophyll; the intercellular spaces are narrow, and no lacunes were observed. No stereome is developed, and the single median vein possesses no parenchyma-sheath, but only a very few leptome-cells and narrow vessels. The leaf-structure is thus almost identical with that of *B. verna*.

In comparing these two species with each other, we notice the following anatomical characters, by which they may be distinguished :

Root without exodermis, *B. verna*.

„ with thick-walled „ *B. lanceolata*.

Stem without sheath of mestome-parenchyma, *B. verna*.

„ with „ „ thick-walled „ *B. lanceolata*.

Leaf with wrinkled cuticle and very open chlorenchyma, *B. verna*.

„ „ smooth „ „ compact „ *B. lanceolata*.

Our genus has thus several histological features in common with *Obolaria* (l. c.), and we notice especially the root-structure, that of a typical mycorrhiza, common to both. Moreover, the stem of *Obolaria* possesses also an endodermis, and shows, like *Bartonia*, the complete absence of stereome ; the mestome-strands are also bicollateral. But the foliage of *Obolaria* is better developed, the leaves being larger and quite fleshy ; nevertheless the structure is much the same, the chlorenchyma being only represented by a homogeneous tissue of roundish cells with no indications whatever of palisade-cells. In regard to the floral structure, the corolla of *Obolaria* shows the presence of nectaries, which do not occur in any of the species of *Bartonia*.

The fact that the roots are mycorrhizae might indicate that these genera, *Bartonia* and *Obolaria*, are saprophytic, but the presence of no small amount of chlorophyll in stems, leaves, and ovaries excludes them from the Holosaprophytes ; they may, however, be regarded as Hemisaprophytes. *Bartonia* and *Obolaria* are near allies so far as concerns the imbricated corolla-lobes and the ovules covering the inner face of the carpels ; but the presence of nectaries in the corolla of *Obolaria*, besides the calyx with only two leaves, which resemble bracts, make the genus very distinct from *Bartonia*. Whether these distinctions may prove sufficient for the removal of *Obolaria* from the Erythraeinae we must leave to the judgement of future monographers of the family. In the present paper we wished only to describe the structural peculiarities as a contribution to the knowledge of these peculiar and interesting plants, which, so far, have been only imperfectly known.

EXPLANATION OF FIGURES IN PLATES XXXIII AND XXXIV.

Illustrating Mr. Holm's paper on *Bartonia*.

(The letters in the figures indicate as follows : *Ep.*, epidermis ; *End.*, endodermis ; *L.*, leptome ; *L**, inner leptome ; *H.*, hadrome ; *M.*, mestome-parenchyma ; *P.*, pith.)

PLATE XXXIII.

- Fig. 1. Three specimens of *Bartonia verna* ; natural size.
- Fig. 2. Same species ; corolla laid open. $\times 2$.
- Fig. 3. Same species ; a stamen. $\times 6$.
- Fig. 4. Same species ; the capsule. $\times 6$.
- Fig. 5. A small specimen of *B. lanceolata* ; natural size.
- Fig. 6. Same species ; inflorescence of a larger specimen ; natural size.
- Fig. 7. Same species ; corolla laid open. $\times 6$.
- Fig. 8. Same species ; a stamen. $\times 18$.
- Fig. 9. Same species ; a flower. $\times 4$.
- Fig. 10. Same species ; two capsules, closed and opened. $\times 6$.
- Fig. 11. *B. verna* ; cross-section of part of stem. $\times 360$.
- Fig. 12. Same species ; cross-section of part of stem. $\times 480$.
- Fig. 13. Same species ; cross-section of part of stem, showing a very small collateral mestome-bundle. $\times 480$.
- Fig. 14. *B. lanceolata* ; cross-section of peduncle, showing a stoma. $\times 480$.
- Fig. 15. Same species ; cross-section of peduncle. $\times 600$.
- Fig. 16. Same species ; cross-section of leaf. $\times 480$.
- Fig. 17. *B. tenella* ; a flower. $\times 4$.
- Fig. 18. Same species ; corolla laid open ; anthers have dropped. $\times 5$.
- Fig. 19. Same species ; capsule. $\times 5$.

PLATE XXXIV.

- Fig. 20. *B. verna* ; cross-section of stem. $\times 480$.
- Fig. 21. *B. lanceolata* ; stoma from the stem. $\times 360$.
- Fig. 22. Same species ; cross-section of basal internode of stem. $\times 480$.
- Fig. 23. *B. verna* ; stomata from the stem. $\times 360$.
- Fig. 24. Same species ; cross-section of one of the higher internodes from about the middle of the stem. $\times 480$.

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Auctor, del.

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19.

17.

Huth, lith. et imp.

Holm, Theodor. 1906. "Bartonia, Muehl. an anatomical study." *Annals of botany* 20, 441–448. <https://doi.org/10.1093/oxfordjournals.aob.a089112>.

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