

Biological and morphological traits of *Mertensia rivularis* (Turcz.) DC. (Boraginaceae) in connection with its ecology

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Summary: The paper presents the results of a comparative study on the structure of the vegetative organs in *Mertensia rivularis* and *M. maritima*. Common structural layout of their epetiolar leaf structure has been proven; particulation of the shoot system has been revealed in both studied species, yet it has been found to be completely absent in the roots of *M. rivularis*. It has also been revealed that in *M. rivularis*, leaf bases contribute to the peripheral zone formation in the annual shoot, forming a so-called ‘leaf sheath’ along the entire organ. Traits of resemblance in the structure of vegetative organs are demonstrated and diagnostic interspecific differences are indicated.

Keywords: Boraginaceae, *Mertensia rivularis*, *Mertensia maritima*, ecology, leaf, leaf sheath, stem, rhizome, root, particulation

Our previous study of *Mertensia maritima*, a crinohalophyte from the supralittoral (spray zone) of the White Sea and the Far East coastline (ALYONKIN & BARYKINA 2020) revealed the presence of specific structural traits connected with adaptations to the environment. Among them, one can note peculiar genesis, macro- and microstructure of epetiolar assimilating leaves, never seen by us in other Boraginaceae, particulation of axial organs, very intense and regularly occurring in the shoot system and sporadically in the root system, the presence of root hairs and endotrophic mycorrhiza in young root tips, etc. All of these traits urged us to continue investigating morphology and anatomy of vegetative organs but now in boreal representatives of the genus *Mertensia* in order to identify the strategy of structural adaptation of the particular species to its particular environment, as well as to reveal the traits of external and internal structures they have in common and differences between species.

Mertensia rivularis was not chosen randomly. This species shows marked resemblance with *M. maritima* in its environmental allocation. However, *M. rivularis* tends to continental areas of boreal eastern Siberian province. There, as VERNOSLOVA (2018) points out, in the vegetation belt of up to 1200 m above sea level, together with large stretches of brushwood (*Dasiphora fruticosa*, *Betula middendorffii*, *Weigela middendorffiana*), meadow plant communities including *Mertensia rivularis* as part of their grass cover are found. The plant grows primarily on temporary streams’ bottoms, on terraces and narrow belts along montane rivers and streams on relatively mobile substrate of rock exposures, on rocky screes (DORONKIN et al. 1997), large gravel- and pebble-beds with shoals’ vegetation; in winter, sites of these kinds accumulate snow cover preventing the ground from deep freezing.

Materials and methods

Herbarium specimens from the collections of Main Botanic Garden named after N.V. Tsytyn, Russian Academy of Sciences [MHA] served as material for the present study: *Mertensia rivularis*

(Turcz.) DC., the Avlandya river valley, Magadan region, North-Even district, 1976, identified by A.P. Khokhryakov and *M. rivularis*, the Vetchichun river, Taigonos peninsula, North-Even district, Magadan region, 1977, identified by A.P. Khokhryakov. To clarify the species' biomorphological description, 22 collection specimens from D.P. Syreishchikov's Herbarium of Moscow State University, Faculty of Biology [MW] have been analyzed. The studied specimens were collected mainly in Yakutia and the Russian Far East (primarily in Khabarovsk territory).

For anatomical research of vegetative organs, softened fragments of herbarium specimens were used. Temporary anatomical preparations were made, and the presence of lignin, starch, lipids and tannins was identified according to traditional anatomical techniques (PROZINA 1960) and in compliance with the recommendations of the microscopic techniques' manual (BARYKINA et al. 2004). Macerated material was utilised to study xylem histology. Light microscope Micromed 3 was used for microscopic observations. Microphotographs of the sections were taken using the light microscope Axioplan-2 and AxioCam MRC camera. Suitable photographs were edited with Adobe Photoshop software. The paper contains scanned images of studied herbarium specimens.

Abbreviations used in Figures. *ac* — air chamber; *ar* — adventitious root; *be* — basal elevations; *clt* — collenchyma-like tissue; *cmb* — cambium; *cpc* — companion cell; *ct* — cortex; *e* — epidermis; *elb* — enlarged leaf base; *fl* — foliage leaf; *gsc* — groups of sieve cells with companion cells; *h* — hair; *hb* — hair base; *ib* — inflorescence bract; *infl* — inflorescence; *iphe* — inner phellem; *lb* — leaf base; *lbd* — leaf blade; *lsh* — leaf sheath; *lt* — loci of anomalous secondary increase in thickness; *ltb* — lateral bundle; *lv* — lateral vein; *m* — mesophyll; *mb* — median bundle; *mr* — medullary ray; *mrb* — midrib; *o* — oil drops; *ophe* — outer phellem; *phd* — phelloderm; *phe* — phellem; *phg* — phellogen; *phl* — phloem; *pl* — paraclade; *plcl* — paraclade covering leaf; *pm* — palisade mesophyll; *pmz* — perimedullary zone; *ppr* — pith parenchyma; *pr* — parenchyma; *prcl* — particle; *prd* — periderm; *prsh* — parenchymal sheath; *pvb* — primary vascular bundle; *rac* — rhexigenous air chamber; *rb* — renewal bud; *rhz* — rhizome; *rl* — rosette leaf; *rsh* — reproductive shoot; *s* — stomata; *sm* — spongy mesophyll; *sp* — storage parenchyma; *svb* — secondary vascular bundle; *svp* — sieve plate; *vs* — vessel; *wlbn* — wing-like leaf base margin; *xl* — xylem; *xpr* — xylem parenchyma.

Results and discussion

Mertensia rivularis is a herbaceous polycarpic plant with a short rhizome (Fig. 1A, B) with its taproot dying off rather early in ontogeny. The rhizome takes an oblique position at moderate depths from the surface; it is epigeogenous, brown in colour, slightly branched at the tip, possessing few vertical or basally decumbent, ascendant, monocarpic shoots. The latter may be dicyclic, less often tricyclic. In the vegetative state, it is typical for them to have a rosette of 3–4 closely located cordate to ovate acuminate 'long-petiolate' leaves with axillary buds. Reproductive shoots, developing from terminal buds in the rosette-like shoots after overwintering, are elongated and covered with leaves all over up to the inflorescence (Fig. 4A). Stem leaves are ovate or oblong; just like the rosette leaves, they have sparse appressed hispid pubescence on the lower side and are scabrous on the upper side due to numerous appressed hispid hairs, slightly enlarged at bases and raised above the epidermis by means of basal elevations (Fig. 5G, H, K). Leaf venation is pinnate-arcuate. Along with the midrib (median vein), markedly protruding on the lower side, 2 pairs of lateral veins are present.



Figure 1. External appearance of *Mertensia rivularis*, a light hygromesophyte. A – herbarium specimen [MHA] of plants in the reproductive stage collected near a montane stream in Taigonos peninsula, North-Even district, Magadan region; B – specimens [MW] of plants from moist rock splits at Dusse-Alin ridge at 1600 m above sea level in Bureya Nature Reserve, Khabarovsk territory; C – fragment of an epigeogenous rhizome and its surface structure: a series of transverse sections illustrating its disintegration resulting in hidden (D–F) and true (G) particulation.

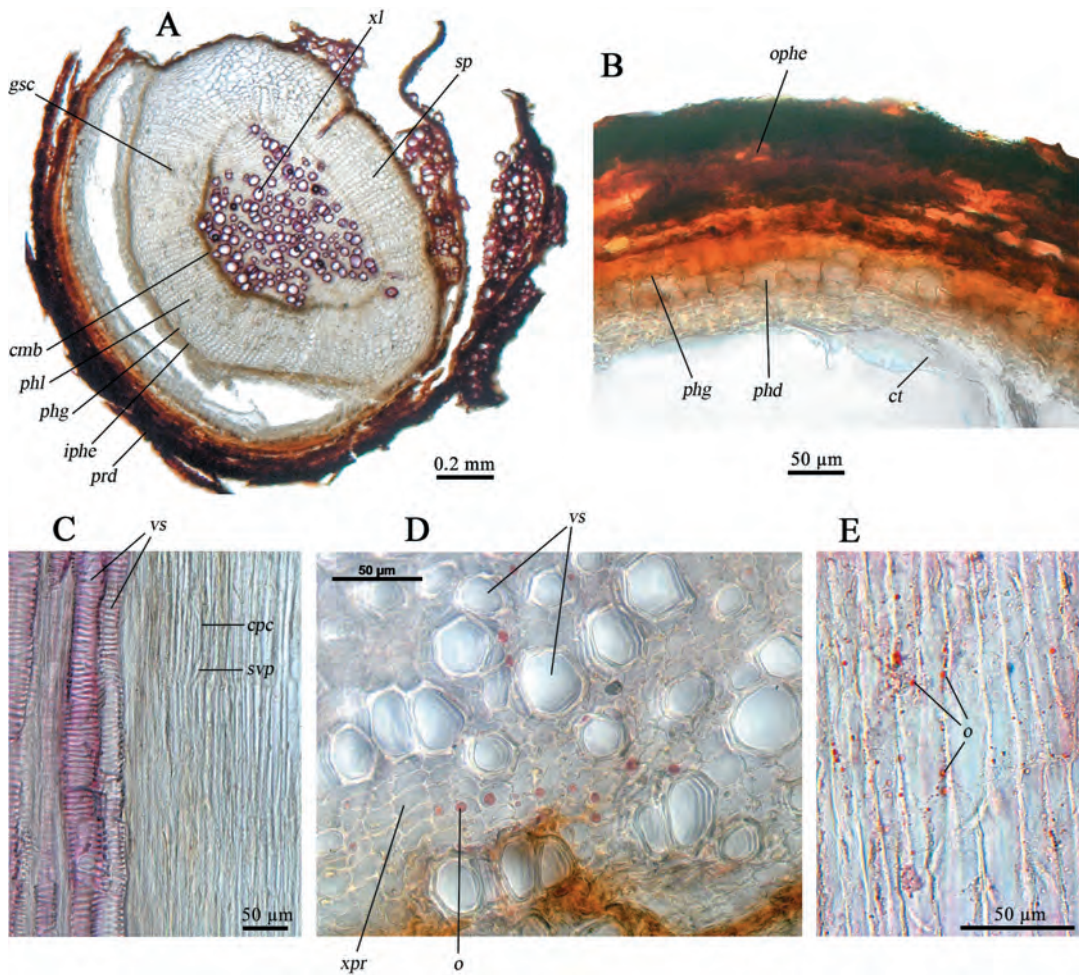


Figure 2. Rhizome particle anatomy. A – transverse section; B – close up of the outer periderm; C–E – vascular system details.

The plant flowers in July to August. Once the morphogenesis of the monocarpic semi-rosette shoot has been completed (late August – early September), the major part of the shoot dies off; however, basal metameres with closely positioned renewal buds, remaining alive (resids), deepen slightly into the substrate and become part of the epigeogenous rhizome. The buds are protected by 3–4 bud scales. This modification of a part of the previously photophilous shoot at its final morphogenetic stage is accompanied by substantial transformations of its microstructure in accordance with the new conditions and functions. The periderm (Fig. 2B) with the phellodermal phellem appears on its surface, while the stele (eustele) undergoes anomalous secondary increase in thickness (Fig. 1C–F), leading to its disintegration into several independent loci of secondary increase in thickness.

Structural disintegration of the rhizome stele in *M. rivularis* in general follows the same pattern as in previously studied *M. maritima* (ALYONKIN & BARYKINA 2020). The particulation is associated with the initiated activity of lateral meristems (cambium and phellogen). Initially, arched strands of vascular cambium originate around secondary tracheary elements of one or two–three adjacent vascular bundles; subsequently, they demonstrate extensive growth until a continuous or almost continuous ring is formed. Usually, 4 or 5 loci of secondary increase in thickness develop, being

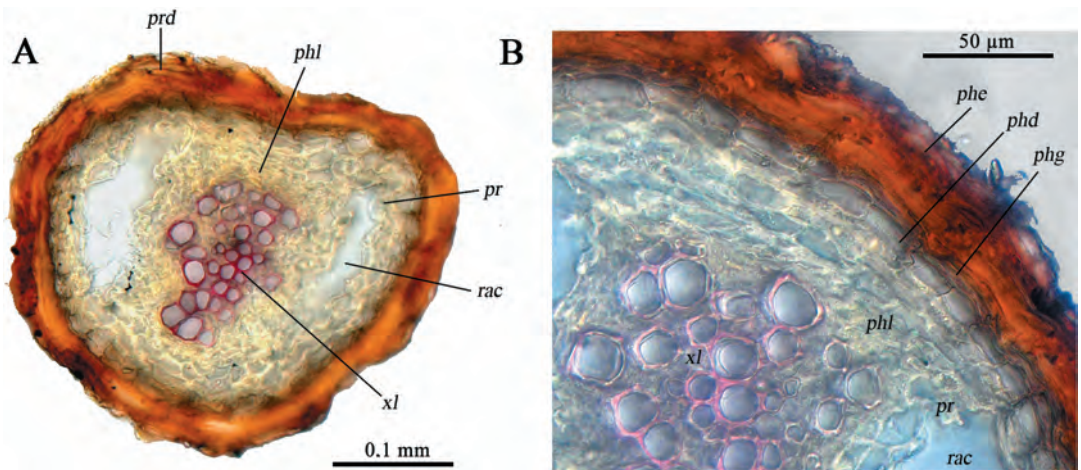


Figure 3. Microstructure of diarch adventitious roots in *M. rivularis* having undergone secondary increase in thickness, with no signs of particulation. A – transverse section; B – fragment of the transection at high magnification.

protected by the potent outer periderm (Fig. 1D–F). On the surface of emerging particles, phellogen is found to differentiate as a result of dilation and proliferation of phloem and xylem parenchyma cells. It forms a ring of inner phellem.

While the particulation patterns in both *Mertensia* species appear to be very similar, a number of differences can also be noted. Thus, in *M. rivularis*, a complete longitudinal rhizome split occurs spontaneously and quite rarely (Fig. 1G), however, hidden anatomical signs of particulation can be determined at rather early morphogenetic stages. The species is known to have primarily incomplete particulation; external signs of disintegration can sometimes be present as visible longitudinal grooves and fissures, where interfascicular parenchyma cells have been lysed or died (Fig. 1C). Yet, the observations of many herbarium specimens have shown that rhizomes in some mature *Mertensia rivularis* plants split into 3 to 5 cord-like, somewhere connected cords (particles), usually left-hand twisted along the organ's longitudinal axis, so true (complete) particulation may have taken place just as well (Fig. 1B). The particles of *M. rivularis* (Fig. 2A) are round or oval in transverse section, lacking a large area of non-functioning living phloem (characteristic of *M. maritima*), and, given the cambial ring is continuous, the vascular bundles remain collateral, visibly resembling amphicribal ones, but contrary to them, due to the direction of xylem areas, isolated by the inner phellem, the cambium derivatives transform solely into storage parenchyma cells.

The root system of *Mertensia rivularis* showed no signs of particulation. Diarch adventitious roots (Fig. 3) rarely undergo secondary increase in thickness; they possess a well-developed periderm including several layers of phelloid cork, phellogen and large-celled phelloderm; a wide parenchymal zone in the bark is found to have rhexi- and lysigenous air chambers.

The stem structure in *M. rivularis* is of special interest. In a young annual stem of the photophilic elongated shoot of a mature plant (which can be both vegetative and reproductive or flower-bearing), the central part is occupied by a copious parenchymal pith composed of tightly adhering polyhedral cells (Fig. 4D). Eventually, the majority of this tissue, except for the minute-celled perimedullary zone, disintegrates and deteriorates, as a result, an air chamber is formed, so the stem subsequently becomes hollow. The stele includes many (over 20) collateral vascular bundles

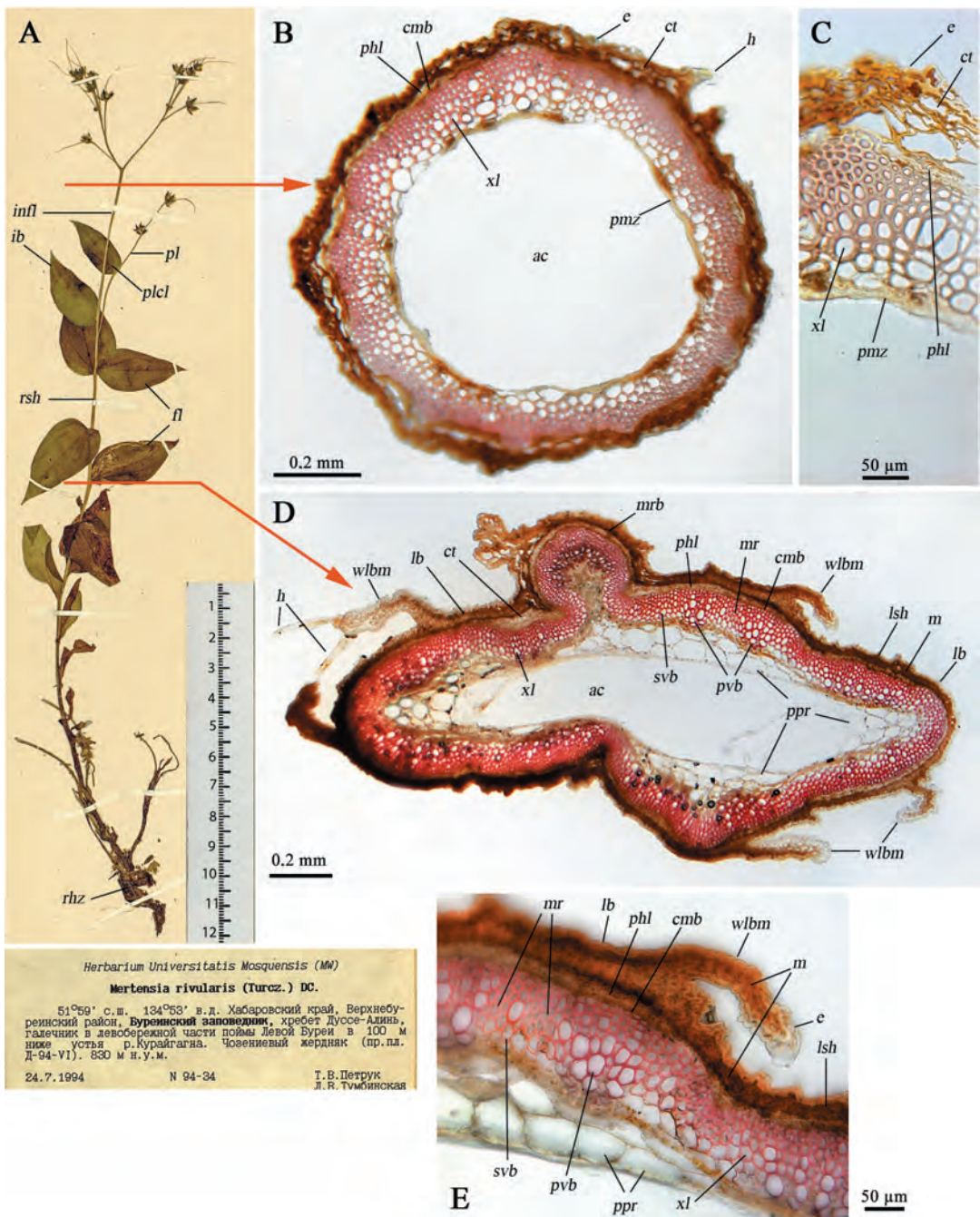


Figure 4. External appearance and stem anatomy of an annual foliated flower-bearing shoot of *M. rivularis*. A – herbarium specimen; a series of consequent transverse sections of the stem: B, C – above the inflorescence bract; D – in the middle of the foliated shoot, near a node; E – in the internode with the conspicuous 'leaf sheath'.

of varying size and origin, arranged in a ring. The vascular bundles are separated by wide primary medullary rays of lignified parenchyma. Large bundles are primary, with pronounced proto- and metaxylem elements at the edge of the perimedullary zone; small vascular bundles, slightly pushed towards the periphery, are secondary; they derive from the interfascicular cambium. In both primary and secondary vascular bundles, only a small amount of phloem is present, the

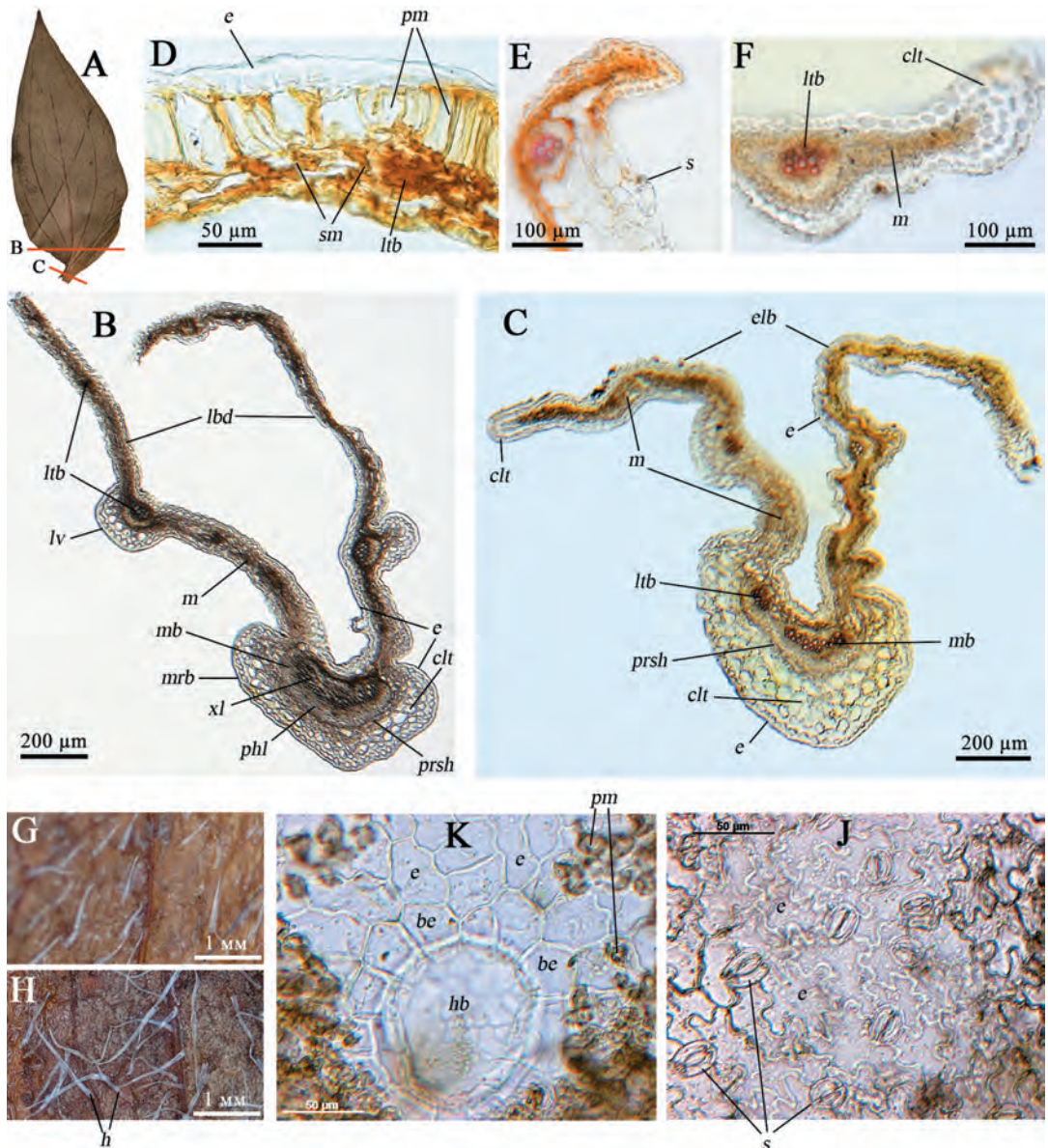


Figure 5. Leaf structure details in *M. rivularis*. A – leaf external appearance; transverse sections of the enlarged (B, D) and cuneate petiole part (C), the edge of the latter with a stoma (E) and collenchyma-like tissue (F); details of leaf blade epidermal complex, pubescence type on the adaxial (G, K) and abaxial (H, J) surface.

latter running as a narrow light stripe above the cambial zone. Histological composition of the vascular bundles in both the rhizome and the annual stem of *M. rivularis* (Fig. 2C–E) resembles that of *M. maritima*. Secondary xylem is represented by rather tightly clustered vessel members of various diameter and length, with helical, helical-scalariform, scalariform-reticulate pitted secondary wall thickening, with simple perforation plates on horizontal or slightly oblique walls, and by axial xylem parenchyma. Secondary phloem comprises small groups of sieve tube members with simple sieve plates on horizontal terminal walls, companion cells, all located within copious axial and radial parenchyma; fibers are lacking here as well as in the xylem. Storage parenchyma is found to contain numerous oil drops.

Externally, the stele is surrounded by a layer of a peculiar tissue, formed by descending bases of assimilating leaves, fused with the stem. Protrusion of non-adhering, wing-like leaf margins located near the nodes (Fig. 4D, E) and extending onto the internodes as well as stem anatomy details may serve as an external 'proof' of the leaf bases' involvement in the formation of the annual stem's peripheral zone. This 'leaf sheath' is conspicuous along the entire elongated, annual, foliated reproductive shoot excluding the inflorescence axis and paraclades above the bracts (Fig. 4B, C), where it does not occur. In the shoot's basal metameres, in the peripheral zone above the phloem ring and primary medullary rays, phellogen initiates, producing two to three layers of phellem and several layers of phelloderm. The peripheral layers of leaf origin, isolated by the periderm, soon die off and are shed. The residua retain the fascicular eustele structure.

Foliage leaf blades are very thin, tender and fine (Fig. 5A, B, D). Epidermal cells along the entire leaf are prominent due to their markedly convex, light swollen outer tangential cells, thus giving the surface a minutely wavy appearance. In paradermal sections of the leaf's adaxial and abaxial sides, they are found to be isodiametric and slightly lobed, with straight or somewhat wavy (adaxial side, Fig. 5K) and flexuous or tortuous (abaxial side, Fig. 5J) anticlinal walls. Epidermal complexes include anomocytic stomata and hispid trichomes. The guard cells are somewhat raised above the epidermal cells. The density of stomata per mm² is greater, yet the pubescence is less pronounced on the abaxial side. The pubescence is scabrous-hispid; trichomes are simple subulate, straight or sickle-shaped (Fig. 5G, H), slightly enlarged at the base, each surrounded by a single-layered rosette of relatively small cells.

The mesophyll is dorsiventral (Fig. 5D), on the adaxial side (with one layer of comparatively large cells of palisade tissue) adhering to the lobed cells of spongy parenchyma with the network of sizeable intercellular spaces, composing 2–3 layers. The average palisade coefficient is around 50%. The median vein (midrib) with the vascular bundles and one or two pairs of large lateral veins conspicuously protrudes on the abaxial surface of the lamina, exceeding its thickness 2–3 times (Fig. 5B, C). Near them, the mesophyll appears to be interrupted, being replaced by large-celled collenchyma-like parenchyma both beneath and along the margin (Fig. 5F). Smaller veins are fully submerged into the mesophyll. Vascular bundles are surrounded by parenchymal sheaths, brown in colour due to tanniferous content. In the narrowed decurrent petiolate part of the leaf blade, a tendency to the basipetal decrease in palisade tissue differentiation and its replacement by homogeneous mesophyll can be traced. The pubescence density is also found to decrease markedly as well as the stomatal count, however, solitary stomata can be observed up to the leaf base (Fig. 5E). Next to the node, large lateral veins start associating with the midrib, creating a united synthetic strand (or bundle) and enter the stele via the only lacuna (Fig. 4D).

As a result of the present research, great resemblance in morphogenesis and leaf structure of both species was revealed, but differences were also found. In particular in *Mertensia rivularis*, the transition from the enlarged part of the leaf blade to the cuneate petiolar part is more pronounced; additionally, leaf bases embracing the stem up to 1/3 appear to fuse producing a so-called 'leaf sheath' on the stem surface. The contribution of leaf bases in the formation of peripheral stem tissues, on its 'dual nature', 'leaf coating' has repeatedly been pointed out by many botanists, starting from POTONIÉ (1912). According to HOFMEISTER (1851), the stem consists of a homogeneous cylinder and cortex, formed by the leaf bases. Examples of the leaf contribution to the formation of cortex as a special peripheral topographic zone are, in fact, quite numerous.

We could observe it during a microscopic study of a shortened rosette shoot formation process in *Coptis trifoliata* (BARYKINA & LUFEROV 1998) and the formation of an elongated ridged shoot typical of *Berberis* species (BARYKINA 1971). The data obtained on the morphogenesis of *M. rivularis* shoot once again confirm the concept of the shoot as an integrated structural and functional system, in which not only the vascular supply, but also the cortex tissues are in tight contact with the leaves, initiated and emerging on the apex – a dynamic system, changing temporally and spatially.

The resids of *Mertensia rivularis*, transforming into the structure of an epigeogenous rhizome, differ greatly from the aerial metamerous of an annual photophilic shoot due their new functions. Retaining the fascicular eustele structure, they demonstrate markedly reduced lignification and enhanced parenchyma development, an increased number of phelloid phellem layers, higher activity of the vascular cambium and related anomalous secondary increase in thickness, resulting in the organ's longitudinal disintegration. The process of true particulation in the shoot system of *M. rivularis*, contrary to that in *M. maritima*, does not always lead to complete isolation of the particles. Most often it is hidden, when a few fully formed particles of one or two bundles remain protected by the common potent sheath of the outer periderm. Relatively thin adventitious roots of *M. rivularis*, emerging from the rhizome, show no signs of particulation at all. They are diarch and undergo typical secondary increase in thickness quite early; they are found to have a wide parenchymal bark zone, comprising a small amount of sieve elements and two oppositely located air chambers, with a thin periderm layer on the surface.

In the vascular bundles of separated particles, the cambium remains active for a number of years. Thanks to cambial activity, the secondary phloem with a great deal of parenchymal tissues and the secondary xylem increase and renew. Therefore, particulation ensures regular supply and renewal of vascular and storage tissues in the rhizome, while in case of full detachment of the particles with dormant buds in reserve and capable of producing roots, it facilitates vegetative propagation on relatively mobile substrate (BARYKINA 2000). Thus, particulation being “among the most interesting biological events in the nature” as vividly expressed by RADKEVICH & SHUBINA (1935: 19) is quite common in representatives of angiosperm families with different life forms and ecology, including Boraginaceae.

Conclusion

The results of the current research demonstrate certain resemblance in the structure of vegetative organs in *Mertensia rivularis* and *M. maritima*. They include anomalous increase in thickness of the stele, epetiolar leaf type with the lamina enlarged in the upper part and narrowed in the lower one, profound development of parenchyma in the axial organs, absence of special supporting tissues, similar histological composition of phloem and xylem, etc. Meanwhile, interspecific differences have also been revealed. They are related to the life forms as well as to structural morphological and anatomical details of certain vegetative organs. Annual stems of *M. rivularis* are covered with so-called ‘leaf sheaths’ (leaf bases fused with the axis). Leaf blades, just like the stems, are pubescent, fine, with conspicuous, protruding midribs and lateral veins. In *M. rivularis*, complete particulation is less frequent in the rhizome and has never been reported in adventitious roots. Considering its habitat and corresponding structural adaptations, *M. rivularis* should be assigned to the ecological group of light hygromesophytes.

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