

Morphological and anatomical characteristics of *Mertensia maritima* (L.) S.F. Gray supralittoral of the White Sea and Russian Far East coast

Vitaly Y. Alyonkin & Rimma P. Barykina

Summary: Adaptive specialization of *M. maritima* to harsh climatic conditions is reflected in morphological and physiological peculiarities of its vegetative organs. Epetiole assimilating leaf blades are differentiated into a distal (expanded) and proximal (cuneate, narrowed) part with revolute margins, imitating a petiole. The leaf anatomy combines mesomorphic and heliomorphic traits. The presence of salt glands characterizes *M. maritima* as a true crynhalophyte.

The impact of moving sandy and rocky substrate affected the structure and behavior of the plant's axial organs: spiral twisting (into a cord) of creeping shoots, growing parallel to each other, transformation into a rhizome, local fusion and particulation. Longitudinal splitting of axial organs with profoundly developed parenchyma into particles is conditioned by anomalous stele thickening, followed by increased localized activity of lateral meristems (cambium and phellogen), dilation and ray and axial parenchymal cell proliferation as well as formation of the inner phellem. The particulation regularly occurs in shoots and sporadically in roots; in the latter, it is often incomplete (hidden). Particles of the shoot origin, with the bud reserves and capable of root formation, when completely detached, can perform the function of optional vegetative propagation on the moving littoral substrate.

In the thin roots, together with root hairs, pronounced hyphae of endotrophic mycorrhizae have been found.

Keywords: Boraginaceae, *Mertensia maritima*, morphology, anatomy, crynhalophyte, leaf, stem, salt glands, rhizome, root, natural grafting, particulation, endomycorrhizae

Mertensia maritima is a tap-rooted halophyte found on the seashores of Europe, Asia and North America, growing on moving substrates of sand and pebbles in the conditions of pronounced soil salinity (SCOTT 1963). Being the northernmost representative of Boraginaceae adapted to living in harsh edaphic and climatic conditions of the Far North, *M. maritima* has become the object of comprehensive studies by many botanists. Brief information on the plant's external appearance, structure of vegetative and reproductive organs and early developmental stages is presented in papers of SCOTT (1963), LID & LID (2005), AIKEN et al. (2007) and SKARPAAS et al. (2007). Details of *M. maritima*'s ontogeny and morphogenesis in the conditions of Russian Far East were relatively thoroughly described by SHIBNEVA (2008), and some specific traits of photosynthetic and stomatal apparatus in leaves, connected with the species's geographical distribution by BURKOVSKAYA & KHROLENKO (2015). Among papers dealing with microstructure of vegetative organs and its changes in the course of ontogeny, a detailed review by SKUTCH (1930) "Repeated fission of stem and root in *Mertensia maritima* – a study in ecological anatomy" deserves special attention. The author provides the results of a thorough study of age-related transformations in the anatomy of axial organs, leading to their particulation (fission). This process appears to start as early as in one-year-old plants grown from seed late in the vegetation season and markedly increases as the plant ages. It is connected with anomalous secondary increase in thickness: in the vascular bundles, an intra-xylem cambium and its derivatives are shown to form, along with the formation of the inner periderm. According to the author, the particulation (fission) takes place

regularly in newly developing shoots, this eventually leads to the formation of a thick cord-like structure; the process occurs sporadically in the tap root, too, as well as in some well-developed lateral roots.

However, records of *M. maritima*, available to date, are apparently insufficient for compiling its comprehensive biomorphological and structural portrait. Many significant aspects have not been covered, such as macro- and microstructural transformations in the shoot system ontogeny, leaf anatomy and morphogenesis, microstructure of stems, rhizomes, roots, processes of natural fusion of rhizome branches, etc. Additionally, some records available are found to have certain inaccuracy, e.g. indication of wax glands present in leaves or inclusion of the species into the category of salt-accumulating halo-succulents (BURKOVSKAYA 2009; BURKOVSKAYA & KHROLENKO 2015) or vegetative propagation by root parts (HACKNEY 2018).

The aim of the present paper is to enlarge, enrich and clarify the existing information available about the structure and functions of this extremely interesting species of *Mertensia*, populating moving substrates in the tidal zone of the White Sea and Far East coastlines, by using our original data.

Materials and methods

Samples of *M. maritima*, collected by A.G. Devyatov in spring and summer of 2017 at the White Sea coast in Kandalaksha district and by T.E. Kramina in summer 2019 at the littoral of Russky Island (Far East), were provided for research, for what the authors are much indebted to the collectors. Also, to clarify the biomorphological characteristics of the species studied, herbarium specimens from D.P. Syreishchikov Herbarium of Moscow State University, Faculty of Biology [MW], Main Botanic Garden named after M.V. Tsitsin [MHA] and Botanic Garden of the Botanical Institute named after V.L. Komarov [LE] were analyzed.

Anatomical studies of vegetative organs were conducted according to traditional anatomical techniques (PROZINA 1960; BARYKINA et al. 2004) and samples were examined at freehand longitudinal and transverse sections. For xylem histology studies, macerated material was used. Stomatal density (number of stomata per mm²) is the arithmetic mean of 30–40 measurements. The external appearance of plants was photographed by iPhone X camera; anatomical microphotographs of leaves and axial organs were taken by means of the light microscope Axioplan-2 and AxioCam MRc camera. Suitable photographs were edited using Adobe Photoshop CS6 software. Photos of plants from the Sea of Okhotsk (Kamchatka area) shoreline were kindly provided by Boris Bolshakov, for what the authors are thankful to him.

Abbreviations used in Figures. *abd* – apical bud; *as* – anastomose; *bdt* – bud trace; *bpr* – bark parenchyma; *ck* – cork; *cb* – connecting bridge; *cmb* – cambium; *cpc* – companion cell; *crp* – cortical parenchyma; *cts* – connecting tissue; *cvb* – collateral vascular bundle; *e* – epiderm; *ein* – elongated internode; *end* – endoderm; *epb* – epiblem; *esh* – elongated shoot; *exd* – exoderm; *fh* – fungal hyphae; *gr* – granules; *gsc* – groups of sieve cells with companion cells; *hfs* – hyphae-like fungal structure; *inf* – inflorescence; *iphe* – inner phellem; *irzb* – isolated rhizome branch; *l* – assimilating leaf; *lb* – leaf base; *lbd* – lateral bud; *lbl* – leaf blade; *lc* – lacuna; *lvb* – lateral vascular bundle; *m* – mesophyll; *md* – mesoderm; *mvb* – median vascular bundle; *nphl* – non-functioning phloem; *pc* – primary cortex; *phe* – phellem; *phl* – phloem; *phlp* – phloem parenchyma; *pm* – palisade mesophyll; *pphl* – protophloem; *prc* – particle; *prcl* – pericycle; *prd* – periderm; *psb* – parenchymal

sheathing of vascular bundles; *pth* – pith; *pxl* – protoxylem; *rap* – ray and axial parenchyma; *rh* – root hairs; *rhz* – rhizome; *rlm* – revolute leaf margins; *rlc* – rosette-like complexes; *rt* – root trace; *rz* – rhizome branch; *sc* – scales; *sg* – salt gland; *sin* – shortened internode; *sm* – spongy mesophyll; *sp* – sieve plate; *spc* – suberized phellem cells; *ssc* – sub-stomatal cavity; *ssh* – shortened shoot; *st* – stomata; *stm* – sieve tube member; *v* – vessel; *va* – vegetative apex; *vsb* – vascular bundles; *xl* – xylem.

Results and discussion

Shoot system of *M. maritima* (Fig. 1A–F) is represented by numerous shoots: branching off the markedly thickened hypocotyl and basal part of the tap root, vertically oriented monocyclic reproductive ones and creeping anisotropic, semi-rosette, usually dicyclic ones emerging from renewal buds in the lower metamers of the main shoot. Each lodging branch starts growing as a plagiotropic vine with one to three elongated internodes. Only some time later, its bud-bearing apex curves upward forming a rosette with closely located, compact nodes, bearing two leaf formations, the terminal and lateral buds. During the first year, the creeping dicyclic shoot remains vegetative. Late in the vegetation season, cork is found to appear on its surface, making the shoot brown in colour, and storage substances are accumulated in the copious ground parenchyma. As a result, a thin, runner-like, dimorphic sympodial rhizome is formed, which typically functions for 2–3 years. Its shortened zone, bearing buds and being capable of producing roots (Fig. 1F) can separate and live independently as a daughter individual, provided that it is submerged in moist substrate and its elongated, less lasting part deteriorates. Probably, when HACKNEY (2018) pointed out *M. maritima*'s ability to propagate by root system parts, broken off in winter storms when the pebbly substrate moves, he confused the modified shoot with the root.

During yearly spring sympodial renewal, often two to four clustered lateral buds of the creeping runner's (Fig. 1G) shortened zone begin to grow together with the main bud. Shoots emerging from these buds grow parallel to each other and increase in number due to particulation. Cases of spiral twisting into a triple cord-like structure have been reported, apparently due to repeated impact of unstable substrate of sand and pebbles as well as to the occasion of stem fusion at points of contact (Fig. 3D); fused sites are a few mm long, the stems further diverging and developing independently again. Despite the widespread process of natural stem and root fusion in the plant world (KRENKE 1950; LOTOVA & LYARSKAYA 1959), this phenomenon was revealed in Boraginaceae for the first time ever.

In the leaf series of *M. maritima*'s annual shoot, the shift of first scalariform leaves by subsequent green foliage leaves is well seen (Fig. 2A). Ovate to oblong, with somewhat cuspidate tips, leaf blades abruptly transform into a cuneate, linear elongated, decurrent lower zone with revolute margins, which resembles a petiole in appearance. In reality, the foliage leaves are sessile. This standpoint is confirmed by the peculiarity of some of their morphogenetic traits and by the structure of leaves of transitional type, replacing cataphylls, 2 to 3 in number, lacking broadened leaf blade part.

The leaf primordium develops according to PRANTL's (1883) pleuroplastic type. Its apical meristem produces the median vein first, the axial leaf part is elongating acropetally (Fig. 2B). Further on, the lamina itself starts to grow due to the activity of the marginal meristem (two symmetrical bulges). The first three assimilating leaves, emerging from the renewal buds following

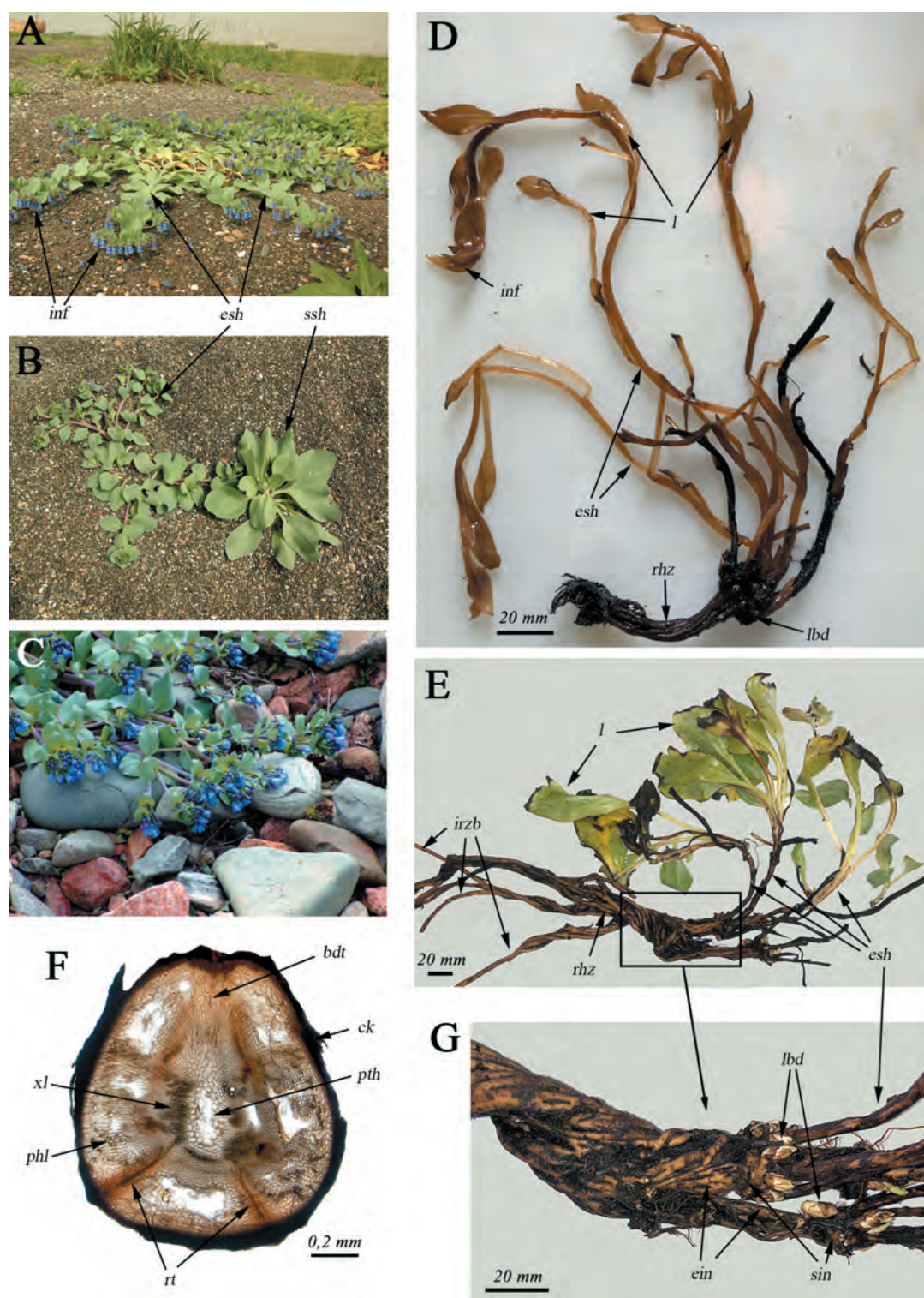


Figure 1. External appearance and shoot system of *Mertensia maritima*, a tap-rooted crynhalophyte. A–C – mature reproductive plants on the Sea of Okhotsk coastline, Kamchatka area (photo: © B. Bolshakov); D, E – samples of *M. maritima* from the White Sea coastline, Murmansk region (D) and littoral of Russky Island, Russian Far East (E); F – transverse section of a node in a rhizome's shortened internode, with traces of two adventitious roots and a lateral bud; G – part of a spirally twisted rhizome in the zone of elongated and shortened internodes, with clustered axillary buds.

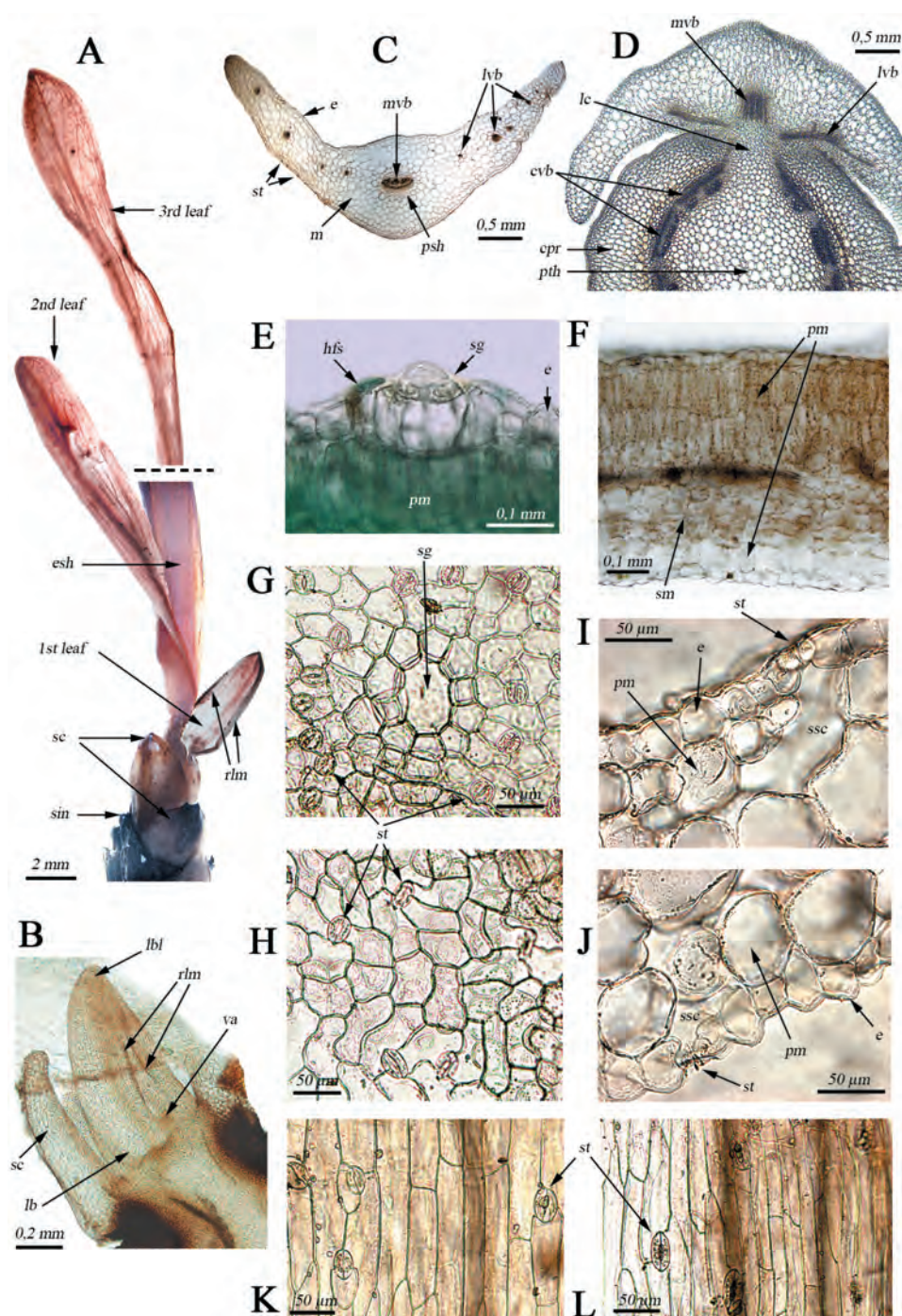


Figure 2. Morphogenesis of an annual shoot and anatomical details of leaves of various formations. A – consecutive shift of scales by the first foliage leaves of transitional type; B – apex of a shortened shoot (brachyblast) with a series of unfolding leaves; C – transverse section through the middle of the petiole-like zone of a foliage leaf blade, with one-layered palisade mesophyll in the wings; D – fragment of a transverse section of an annual shoot's elongated internode, near the node; E–H – transverse sections through the broadened part of the leaf blade, with a salt gland in the upper epidermis (E) and isolateral-palisade mesophyll (F); G, H – paradermal sections of the upper and lower epidermis, respectively. I–L – petiole-like zone of the leaf blade: transverse sections of the adaxial (I) and abaxial (J) sides with poorly expressed palisade cell layer; paradermal sections of the epidermis on the respective upper (K) and lower (L) sides with stomatal complexes.

the scales, have leaf blades of rather peculiar, transitional shape (Fig. 2A). They are markedly elongated, narrow, their margins are revolute towards the median vein, with a cuspidate, slightly thickened tip; although they are not petioles, they resemble them. The leaf morphogenesis type characteristic of *M. maritima* was found in some narrow-leaved representatives of the genus *Eryngium* by DEYNEGA (1903). The petiole usually emerges after the leaf blade formation due to 'intercalary meristem' cell divisions, the latter located basally in the leaf primordium's apical zone, below the marginal meristems. In *M. maritima*, the 'intercalary meristem' remains inactive throughout the entire leaf organogenesis, whereas the cuneate lamina gradually transforms into semi-amplexicaul leaf base. Subsequent foliage leaves differ in a more pronounced lamina's growth breadthwise. As a result, a typical leaf shape is formed at the final developmental stage: ovate or oblong in the upper part and cuneate, narrowed, petiole-like in the lower part. Along with the shape, venation density and pattern also change: loop-like reticulate venation is replaced by an arcuate one, with a small number of tertiary veins.

Morphogenetic peculiarities are reflected in the anatomy of foliage leaves and cataphylls. The scales, embracing about $\frac{1}{3}$ – $\frac{1}{2}$ of the stem base circumference, have large midribs, slightly protruding from the abaxial side and two to four one-bundled lateral veins, possessing parenchymatic bundle sheaths. Epidermal cells are relatively small-sized, with slightly thickened outer tangential walls; no stomata, trichomes or glands are found. Homogeneous mesophyll is represented by 7–10 layers of rounded cells with minute intercellular spaces. Bases of foliage leaves are similar in structure (Fig. 2C). Nodes, bearing both foliage leaves and cataphylls, are unilacunar with leaf traces of 3–9 clustered vascular bundles (Fig. 2D).

As far as the anatomy of the first leaves (not yet fully developed, narrow and petiole-like) and subsequent ones (definitive, with pronounced morphological differentiation into upper, ovate expanded zone, and lower narrowed one with revolute margins) is concerned, even though the overall structural pattern is retained, structural and functional differences are quite conspicuous. The latter are due to uneven growth and duration of development of these parts, venation density and different light conditions.

Blades of foliage leaves are fully covered by thin cuticle and wax. Epicuticular wax gives them glaucescent colour, providing water repellence, preventing the contact of liquids with the leaf surface (see ESAU 1980). The leaves are clearly amphistomatic; minute guard cells are almost at the same level with other epidermal cells (Fig. 2E–H). This being said, epidermal complexes from various parts of the same leaf blade differ in the shape of epidermal cells and appearance of their anticlinal walls; type, location pattern and density of stomata per 1 mm² and gland development, what is well demonstrated in paradermal sections. Adaxial and abaxial epiderm of the expanded upper leaf blade part (Fig. 2E, G) is shown to have mostly isodiametric or slightly lobed cells with straight or wavy anticlinal cells, stomatal apparatus with average density ranging from 97 (abaxial side) to 66 (adaxial side) per mm². In the narrow leaf blade part (Fig. 2I–L), epidermal cells on both sides are oblong with straight anticlinal walls; stomatal complexes are primarily anisocytic, the longer stomatal axis runs parallel to the epidermal cell length; number of stomata per mm² is 36 on the upper and 46 on the lower surface. Secretory trichomes are abundantly spread among epidermal cells on the adaxial side of the leaf blade's wider part, solitary ones are found on the abaxial side, including the narrow part. These trichomes are typical salt glands (Fig. 2E), as it was previously stated by WEIGEND et al. (2016), and not wax glands (BURKOVSKAYA & KHROLENKO

2015) and structurally they are quite similar to leaf glands in *Limonium*. The glands serve to maintain salt balance by means of excreting excessive salt.

In the leaf's expanded part, the mesophyll is isolateral-palisade, on the adaxial side possessing two layers of compactly arranged palisade cells adhered directly to the parenchymal sheaths of numerous vascular bundles or to rounded and lobed cells of 8–12-layered spongy parenchyma (Fig. 2F). On the abaxial side of the leaf, spongy parenchyma is replaced by a layer of relatively short palisade cells, separated by substomatal chambers; these cells contain few chloroplasts. In the leaf blade's narrow part, under less favourable light conditions and with revolute margins, the tendency of basipetal decrease of palisade tissue differentiation can be observed (Fig. 2C), up to the complete replacement by homogenous mesophyll in the lowermost, the narrowest part of the lamina. A similar pattern is found in the leaves of transitional type, their blades possessing poorly differentiated mesophyll and a relatively small number of vascular bundles; this fact is determined by their accelerated morpho- and histogenesis.

Adaptations revealed at anatomical, morphological and physiological levels count against considering *M. maritima* a salt-accumulating halophyte and suggest treating it as a crynhalophyte – a plant absorbing salts in great amounts, which results in high osmotic pressure, but getting rid of excessive salt by excreting it through special glands on its leaves. Leaf microstructure combines mesomorphic and heliomorphic traits.

Studies of the natural stem grafting that takes place at both the level of shortened parts of the shoot, where bases of clustered buds (at different stages of post-embryonic developmental stages) fuse (Fig. 3A) as well as the level of elongated ones, have demonstrated that this process is facilitated by the peculiarity of their anatomical structure. The young stem (Fig. 2D) is found to have a thin-walled epiderm covered by cuticle and wax, a wide zone of parenchymal cortex and pith, a ring of vascular bundles (9–11) located far apart with phloem predominating in them, a 4–5-layered cambium zone, secondary xylem and phloem with parenchyma, no specialized supporting tissues and a periderm with relatively poorly suberized phellem cell walls (the phellem is revealed at the end of the first vegetation season in the basal shoot metamers persisting as part of a branched sympodial juvenile rhizome). Contrary to the photophilic shoot, the phellem is also found in the perimedullary region in the 2 years old rhizome (Fig. 3B), isolating the central part of the pith that dies off.

The secondary xylem in the stem is composed of vessel members varying in length and diameter, with spirally or scalariform-spirally thickened walls, simple perforation plates on horizontal cell walls (Fig. 3C). In the stem parts having undergone physical impact, followed by nutation, tracheary elements in curved xylem strands are usually long, spirally thickened, with small lumens and skewed end. The secondary phloem comprises sieve tubes with simple sieve plates on their terminal horizontal walls, situated in small groups amongst copious parenchyma as well as companion cells, axial and ray parenchyma; no fibers are present.

The above-mentioned traits of stem and rhizome microstructure favour their fusion. The latter is combined with wound healing. Due to friction of two stems tightly pressed to each other, the contact between them is established at small areas embracing both easily proliferating parenchymal cells and vascular elements (Fig. 3D–F). Adjoining wound tissues form a connective layer, its cells giving rise to new differentiating cambium strands, connecting vascular cambia of both stems, establishing continuity of their vascular system (Fig. 3G).

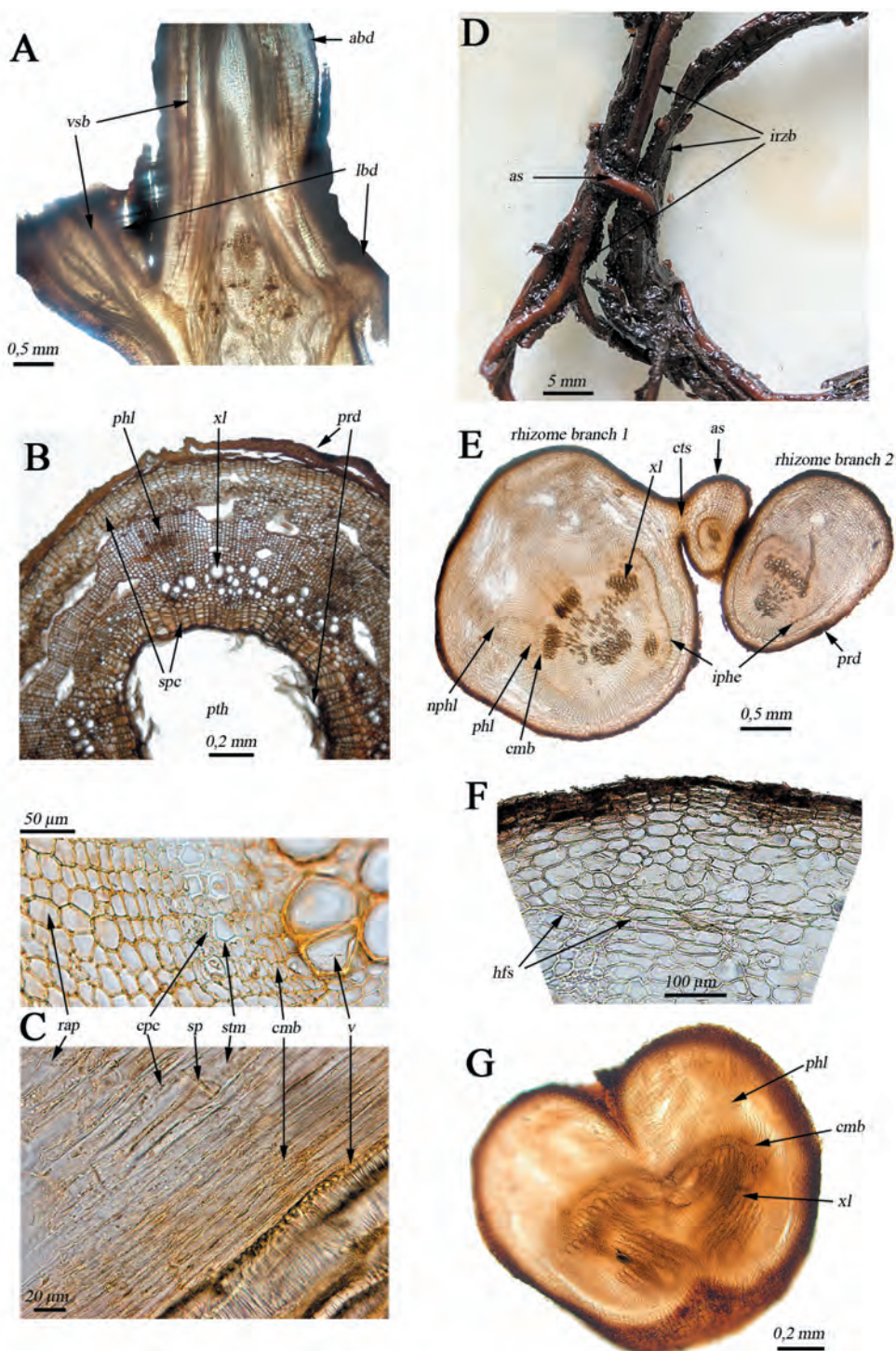


Figure 3. Natural localized stem grafting, with some anatomical details. A – basal fusion of buds at different developmental stages, in the zone with nodes brought close together; B – segment of an elongated internode in a degrading biennial rhizome; C – fragment of both transverse and longitudinal sections of a vascular bundle in an elongated annual aerial shoot; D – mutual fusion of the biennial rhizome's branches at the internode level, by forming an anastomosing structure; E – transverse section of the site, where two parallel-growing shoots are fused by the connecting anastomosis; F – cross section of the shoot particle with hyphae-like structures in the cortical part; G – unification of parenchymal and vascular elements in fusing stems.

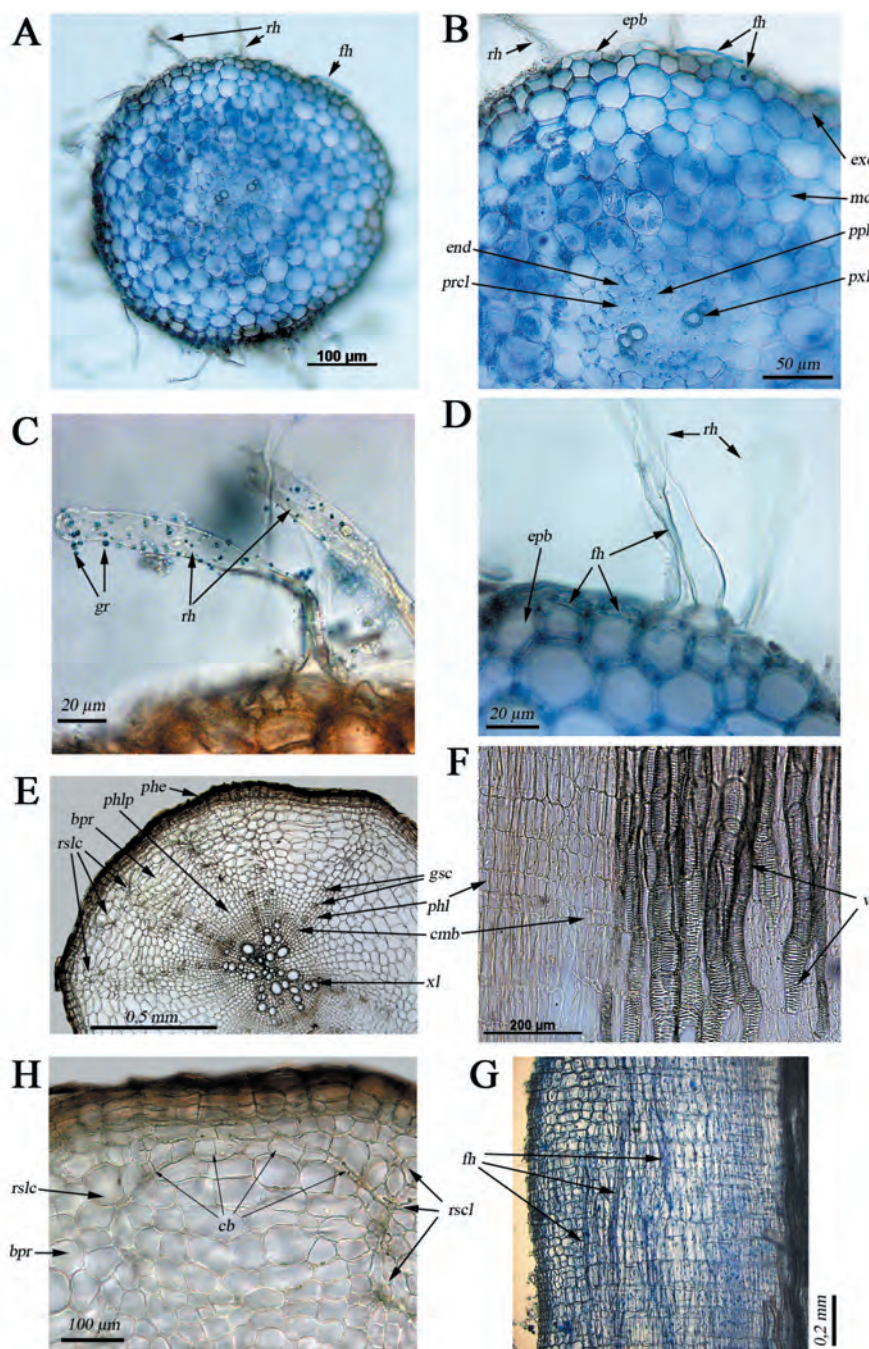


Figure 4. Peculiarity of lateral root anatomy. A–D – root of primary structure near the absorption zone, with root hairs and endotrophic mycorrhiza; E–H – fragment of a root having undergone secondary thickening, its vascular system and pronounced rosette-like structures in the bark parenchyma.

The tap root, lateral and adventitious roots are diarch. A thin root near the absorption zone (Fig. 4A, B) appears to possess the epiblem with root hairs, often containing, together with the nucleus, finest inclusions of unknown origin in the wall-adhering layer of the cytoplasm (Fig. 4C). The epiblem is underlaid by a layer of relatively large exodermal cells, with their cell walls naturally stained brown. The mesoderm comprises up to 6 layers of rounded cells with a

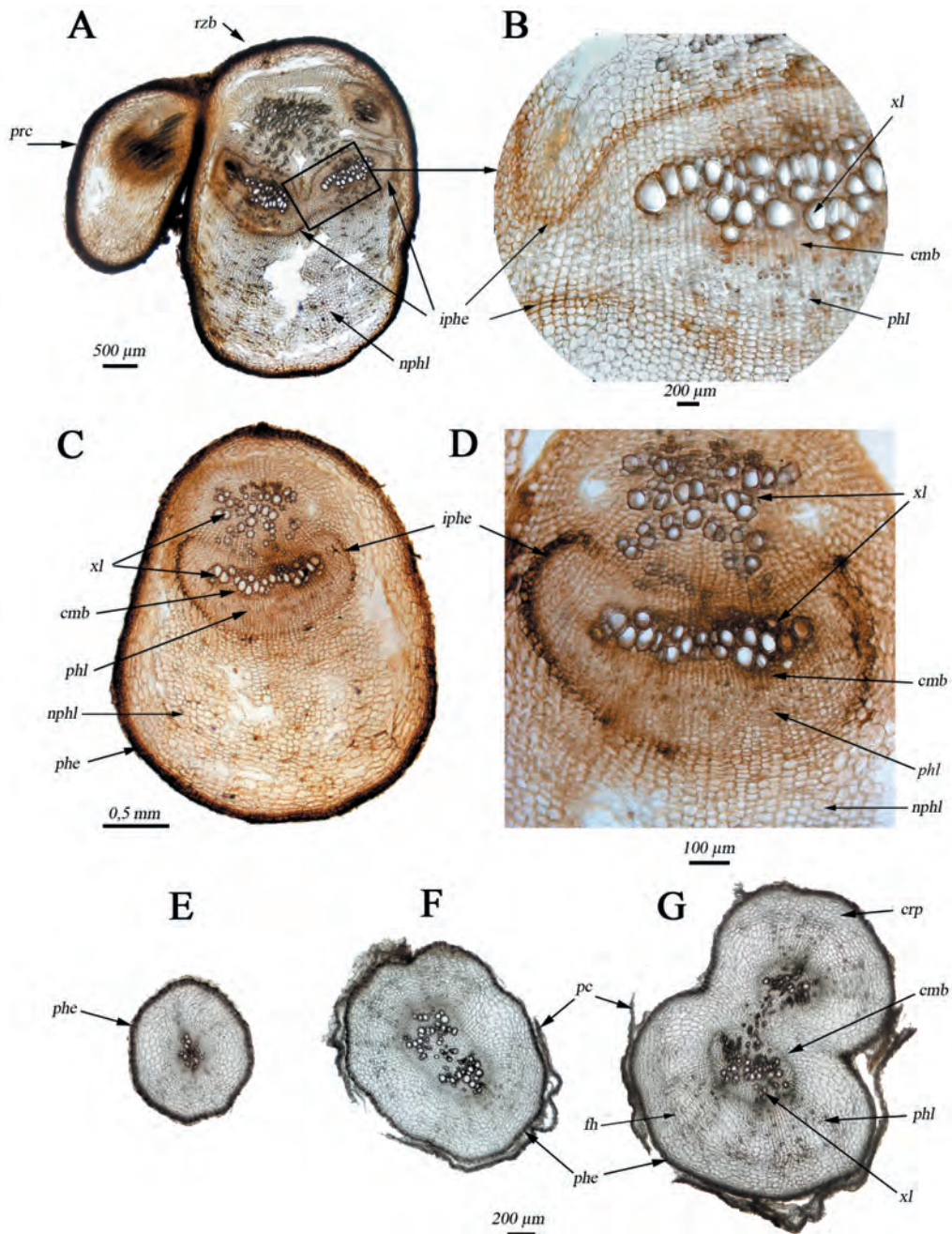


Figure 5. Anatomical structure of particulating rhizomes and roots. A – three-bundled branch of a biennial rhizome, with traces of anomalous secondary increase in thickness and partially detached thinner one-bundled branch; B – initial stage of inner phellem formation around the sites of xylem elements and functioning phloem ones; C, D – separated particle with inner and outer phellem, the functioning cambium and a wide zone of non-conducting phloem; E–G – consecutive stages of anatomical transformations in a diarch root prior to its particulation.

system of tiny intercellular spaces, arranged in radial rows. The entire cortex is penetrated by branching endomycorrhizal mycelium; the presence of mycelium on the root surface has also been noted (Fig. 4B, D). The endodermis cells have casparian strips. One-layered pericycle is represented by minute cells with no signs of division.

Since the stele undergoes secondary increase in thickness early and the phellogen originates in the pericycle, the cortex dies off and is cast off (Fig. 4E). On the root surface, phellem with thin cell walls and tannins in the outer layers becomes visible. Secondary phloem, much parenchymatized, predominates. Member of 2–3 sieve tubes with simple sieve plates and companion cells, located nearby, form some small groups, radially arranged amongst the cells of copious phloem parenchyma (Fig. 4E). The secondary xylem includes scalariform and pitted vessels with simple perforation plates and xylem parenchyma, its thin walls are not lignified (Fig. 4F). Discernible cambial zone consists of up to 5 cell layers. The outer parenchymal bark zone (of phellodermal or pericyclic origin) is found to contain fungal hyphae (Fig. 4G) at the border with the phloem zone; along with the nucleus, in the parietal cytoplasm zone of these cells, very small prismatic and rhombohedral crystals can be seen. Sometimes these complexes can be connected by small bridges (Fig. 4H). Similar structures are present, in a smaller number, at the periphery of the stem or rhizome bark zone. One cannot exclude that they are peculiar schizogenous secretory structures with a small central intercellular space or cavity, lined with the epithelium. This suggestion requires a more thorough investigation to be proven.

Characteristic anatomical traits of roots in *M. maritima*, growing in conditions of excessive moisture, are the lack of typical aerenchyma or air cavities; yet there, as well as in the stem, a system of minute intercellular spaces is found. Additionally, when anatomical cross sections of axial organs have just been made and placed in water, at the very first moment, a great amount of evanescent air bubbles appears. This may serve as an indirect indication that the plant has an effective ventilation system which has not been discovered yet. Relatively poor development of intercellular spaces and air cavities has been recorded in roots of many rooting hydrophytes, e.g. *Ranunculus peltatus* Schrank (BARYKINA 1988), that, according to some scholars (LAING 1940; ANTIPOV 1964) can apparently be connected to the ability to survive, especially in winter time, thanks to anaerobic respiration.

In stems, rhizomes and roots of *M. maritima*, particulation is well demonstrated; that is not the senile particulation (SHIBNEVA 2008), but the true one, starting as early as in virgin plant individuals and being accompanied by anomalous secondary increase in thickness of the stele in the organ with profound parenchyma development (Fig. 5). Numerous literature sources indicate that it is expressed by the separation and extensive growth of vascular cambium around tracheary elements of the secondary xylem belonging to one or, in some cases, two to three closely located vascular bundles simultaneously. Tips of each curve (Fig. 5A, B) connect to form an almost continuous ring due to proliferation of ray and axial xylem parenchyma cells; as a result, several sites of secondary meristem are formed. On the surface of detached particles, comprising one or two to three vascular bundles, phellogen is differentiated owing to extensive cell divisions in the adjacent parenchyma layer. The phellogen appears to produce the inner periderm with slightly suberized cell walls. Probably, this structural trait of the phellem is responsible for the preservation of the wide zone of living, non-conducting phloem in the particles. Meanwhile, the outer periderm apparently provides secure protection for the rhizome branches and roots from the negative influence of the salt solution, diurnal and seasonal fluctuations of air and soil temperature. Interfascicular parenchyma cells eventually get destroyed and disintegrate by lysis. In the vascular bundles in separated particles, the cells of ray, xylem and phloem parenchyma keep dividing and growing intensely, pushing the sites with vascular elements apart, which leads to the formation of new particles. In relation to this regularly repeated process, spirally twisted (into a

cord) rhizomes of relatively young *M. maritima* individuals possess a great number of branches, each of them being an individual particle (Fig. 5C, D) with the reserve of buds and capable of root formation. The impact of the moving substrate on the rhizome can cause its branches (particles) to become autonomous and their subsequent life as independent plants (BARYKINA & ALYONKIN 2019). This kind of optional vegetative propagation directly results from the species's adaptive specialization to the supralittoral conditions in northern aquatic areas.

Unlike the shoots, a tendency to hidden particulation can quite often be observed in the roots of various diameter, excluding the tap root and the thickest lateral roots. Consecutive stages of anatomical transformations, preceding the particulation itself, are presented in Figure 5 E–G. They are rather similar to those observed in the stem, with the only difference that fully formed particles do not completely separate yet and remain covered by the common outer periderm. A similar peculiarity of secondary growth in the roots as in *M. maritima*, accompanied by the formation of discrete concentric open vascular bundles and hidden capability to particulate has been recorded in some tuberous species of *Aconitum* L. (KUMAZAWA 1937; BARYKINA et al. 1977). Considering particulation as the process of longitudinal splitting of axial organs into separate living parts, the particles capable of independent development after detachment were firstly described by JOST (1890). Its widespread occurrence in the nature must be pointed out. The particulation occurs in many angiosperm families of different habitats, ecology and life forms. It is most frequent in steppe, semi-desert and desert plants, in some representatives of alpine flora and much less often in forest mesophytes and seaside halophytes. But regardless of the plant's taxonomic position, structural transformations, resulting in the particulation of an axial organ, follow the same general pattern (PFEIFER 1926; RADKEVICH & SHUBINA 1935; KUMAZAWA 1937; BULGAKOV 1944; SHALYT 1965; BARYKINA & GULANYAN 1974; BARYKINA et al. 1976, 1977; BARYKINA 2009).

Thus, in the course of the present study, peculiarity of foliage leaves in *Mertensia maritima* has been revealed. They were found to be epetiolar (sessile). Their laminae are differentiated into a flattened and expanded distal part and a narrowed proximal one, the latter with revolute margins imitating a petiole. In the leaf's macro- and microstructure, traits of specific adaptations to the coastal habitat are clearly expressed: thick epicuticular wax coating, partly revolute margins, fully amphistomatic lamina with densely located stomata, dense venation pattern and isolateral-palisade mesophyll in the expanded leaf blade part. The above listed microstructural features serve to protect the leaf from bright sunlight and dehydration caused by saline water, strong winds and high solar radiation. The presence of multiple salt glands on the leaf's adaxial side characterizes *M. maritima* as a typical crynohalophyte.

Moving substrate of sand and pebbles affects the growth pattern of creeping shoots and rhizomes, making them intertwine, twist, fuse locally or split longitudinally. This is facilitated by the peculiarity of anatomy of the axial organs: profound parenchyma development, dilation and proliferation of diffuse and ray parenchyma cells, poor lignifications, absence of specialized supporting tissues, formation of phellem with slightly suberized cell walls. The phellem, as the secondary dermal tissue, has not been reported for other herbaceous Boraginaceae previously.

The particulation, taking place due to anomalous stele thickening, accompanied by increased local cambial activity and phellem formation, very often occurs in the stem (and is very active) and sporadically in the root. In thin roots, root hairs and hyphae of endotrophic mycorrhizae are

pronounced. Structures visually resembling fungal hyphae are found in the stem (Fig. 3F) and even in assimilating leaves. However, their true nature can only be identified by a mycologist.

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Address of the authors:

Vitaly Y. Alyonkin (corresponding author) *

Rimma B. Barykina

Department of Higher Plants

Faculty of Biology

Lomonosov Moscow State University

Vorobyevy Gory 1 (12)

119992 Moscow, Russia

E-mail: boraginaceae@mail.ru *

barykina28@mail.ru

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