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Anatomy of the roots of some northern hemiparasites (Orobanchaceae)

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Key words: *Bartsia alpina*, *Castilleja lapponica*, *Pedicularis lapponica*, *Pedicularis sceptrum-carolinum*, *Rhinanthus minor*, *Scrophularia nodosa*, haustorium.

Summary. The root structure and the haustorial formation of 5 northern hemiparasites: *Bartsia alpina*, *Castilleja lapponica*, *Pedicularis lapponica*, *Pedicularis sceptrum-carolinum*, *Rhinanthus minor* subsp. *groenlandicus* (Orobanchaceae) have been studied. The autotroph *Scrophularia nodosa* (Scrophulariaceae) has been chosen as a control. It is shown that the main preconditions providing the possibility of rapid haustorium development are the long life of the primary outermost tissue of the root – the rhizodermis that covers the entire length of both young and older roots, and constant readiness of this tissue to form special haustorial hairs, and also an unusual structure of exodermis, which in many details is similar to rhizodermis. The formation of haustorial hairs is one of the earliest structural events in haustorium development; the haustorial hairs are long, with a smooth surface. The division and elongation of cells in the outer tissues play a major role in the early stages of endophyte development. The parasitic form of life influence the inner structure of the vascular cylinder that appears as the reduction of phloem conductive elements and the accumulation of large amounts of starch in the xylem. It was found that the haustoria can penetrate not only in the roots but also in the rhizomes of the host plants.

Анатомия корней некоторых северных растений-полупаразитов из семейства Orobanchaceae

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Ключевые слова: *Bartsia alpina*, *Castilleja lapponica*, *Pedicularis lapponica*, *Pedicularis sceptrum-carolinum*, *Rhinanthus minor*, *Scrophularia nodosa*, гаустории.

Аннотация. Изучено анатомическое строение корней и образование гаусторий у 5 видов полупаразитов: *Bartsia alpina*, *Castilleja lapponica*, *Pedicularis lapponica*, *Pedicularis sceptrum-carolinum*, *Rhinanthus minor*, ранее относимых к семейству Scrophulariaceae, а в настоящее время перенесенных в Orobanchaceae, и одного непаразитного автотрофа – *Scrophularia nodosa* (Scrophulariaceae), с целью выявления структурных особенностей, отражающих самые ранние этапы перехода растений к чужеядности. Объекты изучены как с помощью светового, так и сканирующего электронного микроскопа. Показано, что долгая сохранность и несколько необычное строение наружных тканей корня – ризодермы и экзодермы являются главной предпосылкой возможности быстрого формирования гаусторий. Поверхностные ткани способны к постоянному делению и растяжению. Ризодерма, образующая гаусториальные волоски, ответственна за начальные стадии развития гаустории. Гаусториальные волоски представляют собой длинные извитые выросты с гладкой поверхностью, они могут возникать как на молодых, так и на более старых корнях разных порядков ветвления, причем на любой их части. Наружные ткани участвуют также и в дальнейшем процессе развития гаустории, в том числе в формировании эндофита – погруженной в органы хозяина части гаустории. Результатом перехода к чужеяд-

ности, возможно, являются такие микроструктурные признаки корней, как наличие у некоторых видов в центральном цилиндре многослойной паренхимы над проводящей флоэмой, слабо выраженная архность корней, большое количество крахмала в ксилеме. Выявлена возможность проникновения гаусторий не только в корни, но и в корневища растений-хозяев.

Introduction

Usually the main interest of the scientists when they study the ecological group of hemiparasitic plants concern the organs of attachment to the host – i. e. haustorium that is the final step in the adaptive evolution of plants which is using another plants as the special nutrition (Metcalf, Chalck, 1950; Piehl, 1963; Dobbins, Kuijt, 1973a, b; Kuijt, 1969; Heide-Jorgensen, Kuijt, 1995; Matthies, 1997; Lonser-Goshen et al., 1998; Calladine, Pate, 2000; Cameron et al., 2005; Cameron, Seel, 2007). Thus, very little attention is paid to the “ordinary” structure of underground vegetative organs – roots and rhizomes, though their composition obviously should reflect the earliest stages of plants transition to parasitism (Khan et al., 2009). The intermediate links in the chain of adaptive evolution autotroph-hemiparasite-parasite should be found in the structure of the roots. The changes that occur in the anatomy of the underground organs of hemiparasitic plants compared with autotrophs are the key to understanding the causes and stages of a structural adaptation to parasitism.

Data on the root anatomy of hemiparasites are extremely scarce. In the “Anatomy of the dicotyledons” (Metcalf, Chalck, 1950) only a few phrases are written about the roots of hemiparasites and even this description mostly concerns the structure of the haustoria. A little information about the roots can also be found in “Parasitic Orobanchaceae...” (Joel, Gressel, Musselman, 2013). So, the new information on this topic is of current interest.

Materials and Methods

Six species were studied: autotroph *Scrophularia nodosa* from the family Scrophulariaceae and hemiparasites *Bartsia alpina*, *Castilleja lapponica*, *Pedicularis lapponica*, *Pedicularis sceptrum-carolinum*, *Rhinanthus minor* subsp. *groenlandicus*, now included in the family Orobanchaceae. Hemiparasitic plants were collected in late August in 2013–2014 at the foot and in the tundras of Khibiny mountains near the Polar-Alpine Botanical Garden (Kirovsk, Murmansk region), *Scrophularia nodosa* – in early July 2014 in the park “Fili” (Moscow). The roots of the plants were photographed and then fixed in 75 % ethanol.

Roots were prepared for light microscopy differently. Cross sections were cut with a safety razor by hand and with a rotary microtome. Root samples were fixed as follows: 70 % ethanol; 75 % ethanol with eosin; 85 %; 95 %, 100 % ethanol; 100 % ethanol : chloroform (3 : 1); ethanol : chloroform (1 : 1); ethanol : chloroform (1 : 3); chloroform. After fixation, roots were transferred into the crucibles with Hystomix and placed in a thermostat at 57 °C for 2 weeks. Then the plant material was cut with a rotary microtome. The sections were mounted on slides. Dried slides were stained in a Thermo SCIENTIFIC Varistan Gemini ES with the dyes proposed by Aksenov (Barykina et al., 2004).

To examine anatomical details using a scanning electron microscope (SEM), material was fixed in 70 % ethanol, then dehydrated using 96 % ethanol, 96 % ethanol : acetone (1 : 1), acetone and critical-point dried. Dried material was mounted onto specimen stubs using a double-sided tape, coated with platinum and examined using a CamScan 4 DV (CamScan, UK) in the electron microscopy laboratory of biological faculty MSU.

Results

Scrophularia nodosa

Adventive roots – cross section (Fig. 1A)

The exodermis (Fig. 1C) – an outermost root tissue – consists of cells (~25–50 µm in diameter) with thick outer tangential walls. We also observed rhizodermis cells that were collapsed or squashed. The primary cortex is composed of 10–12 layers of parenchyma cells of nearly the same size as the exodermis cells, and small intercellular spaces. The endodermis consists of the relatively small cells (~15–20 x 7–10) with Caspari strips. The pericycle is of more or less large oval cells. The phloem is composed of 3–5 cell-layers, including mainly the conductive elements. The xylem mass consists of wide (~48–50 µm in diameter) and narrow (~10–16 µm) tracheids and vessels and lignified parenchyma. The root has a tetrarch xylem pole pattern, though the primary rays are slightly recognizable.

Rhinanthus minor subsp. *groenlandicus*

The primary root – cross section (Fig. 1B)

The surface tissue of the old root is exodermis. Collapsed rhizodermis cells can be seen somewhere

outside the exodermis. The parenchymatous primary cortex consists of 5–6 layers of relatively large (~30–50 μm) thin-walled cells (Fig. 1D). The cortex of the old root is usually partially collapsed. The pericycle is not clearly identified. The phloem

is 2-layered and forms a discontinuous ring. The xylem consists of conductive elements (~25–52 μm) and lignified parenchyma; the rays of primary xylem are not clearly identified. All cells, including coating and xylem elements, contain starch grains (Fig. 5F).

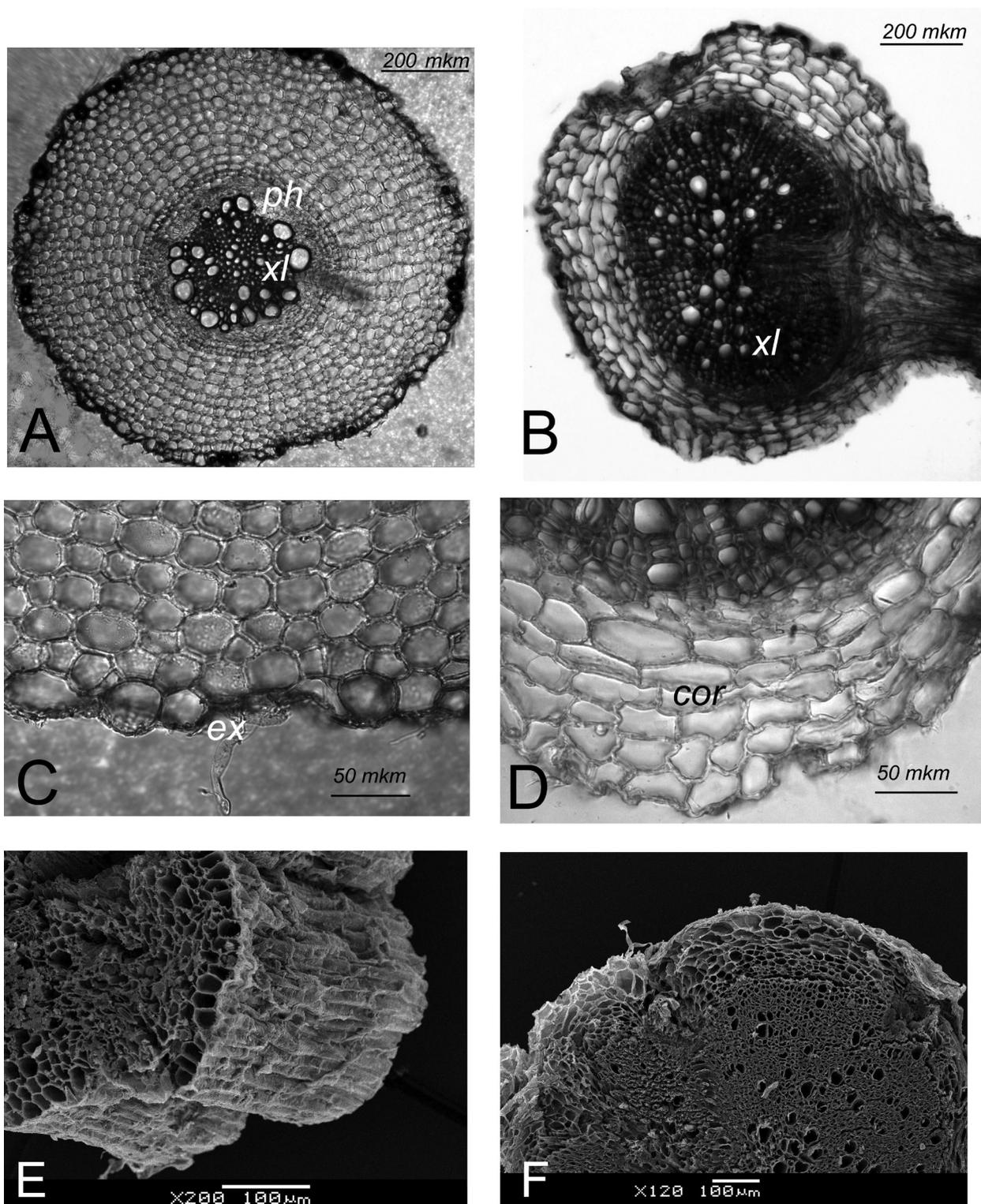


Fig. 1. Root anatomy of *Scrophularia nodosa* and *Rhinanthus minor*: A – cross section of *S. nodosa* root; B – cross section of *R. minor* root; C – exodermis and cortex in *S. nodosa* root; D – cortex in *R. minor* root; E – $\frac{3}{4}$ cross section of *S. nodosa* root (SEM); F – xylem and cortex in the *R. minor* root. ph – phloem, xl – xylem, cor – cortex, ex – exodermis.

Bartsia alpina**Adventive roots – cross section (Fig. 2A)**

The surface tissue of the root is rhizodermis or exodermis (Fig. 2E, F) consisting of elongated actively dividing living cells (~20–30 µm); their protoplasts are granular and dark in color, the outer walls are laminate. On the root surface cells are organized in rows of distinct 2–5-celled strands (~60–90 µm in length, 12–15 in width). The parenchymatous primary cortex is 3–4-layered. The endodermis cells contain dark protoplasts, actively dividing. The wide outer part of the stele is 8–10-layered consisting of regular rows of square or hexagonal parenchyma cells (~12–33 µm) (Fig. 2A, B). The conductive phloem is reduced to a few layers. The xylem includes the wide conductive elements (~23–27 µm in diameter) and small lignified parenchyma cells. In mature roots the xylem pole pattern is not obvious.

Castilleja lapponica**Adventive roots – cross section (Fig. 2C)**

The rhizodermis and the underlying exodermis consist of large oblong thick-walled actively dividing living cells (~20–25 µm) with dark content. On the root surface cells are organized in rows of distinct 2–5-celled strands as in *Bartsia alpina*. The parenchymatous primary cortex is 2–5-layered consisting of densely arranged sometimes compressed anticlinal dividing cells. The outer tissues as well as all the cells of the primary cortex are filled with starch. The endodermic cells are suberized and lignified. The pericycle is multi-layered, consists of square cells. All non-conducting tissues of the stele divide, forming regular rows of square and hexagonal non-conductive parenchyma cells (15–25 µm) (Fig. 2D). The conductive phloem is reduced to a few sites outside the xylem. The xylem is often organized in a specific pattern: the wide conductive elements are replaced by the narrow elements from the periphery to the center. There is also a lignified xylem parenchyma, densely filled with starch. Perhaps some narrow conducting elements are also filled with starch. The number of primary xylem rays is not distinctly visible.

Pedicularis lapponica**Adventive roots – cross section (Fig. 2F)**

The root is covered by the rhizodermis or the exodermis consisting of large dark-colored thick-walled cells (~50 µm) with transverse partitions. The primary cortex is composed of 4–5 layers of thick-walled parenchyma cells (~25–30 µm) filled

with starch, and large intercellular spaces. The endodermic cells are elongated with Caspari strips. The pericycle is single-layered, discontinuous or not clearly expressed. The stele includes a broad outer zone of parenchyma cells and inner greatly reduced conducting phloem. The protoxylem is triarch, but more often the xylem pole pattern is not obvious. The secondary xylem includes wide (~25 µm) and narrow (~12 µm) *tracheary elements* alternating with small parenchyma cells.

In the outer tissues of *P. lapponica* root the hyphae of fungi predefined as the Dark Septate Endophytes have been found.

Thin elongated underground rhizomes (Fig. 3E)

The epidermis is composed of small living cells with thickened outer walls and dark protoplasts. The subepidermal tissue – exodermis has a similar structure to the epidermis, though its cells are much larger. The primary cortex consists of 5 layers of thick-walled cells, and small intercellular spaces. The endodermic cells have Caspari strips. There are several layers of parenchyma cells organized in straight rows between the endodermis and conducting phloem. The leaf breaks are clearly visible in the rhizome nodes (the feature that distinguishes the anatomy of the rhizome from the root, these two organs are very similar in many other details).

The centers of subepidermal periclinal divisions in some areas of the rhizome are similar to those in the roots when the haustorium develops.

Pedicularis sceptrum-carolinum*.*Adventive roots – cross section (Fig. 3A)**

The outermost root tissue is a rhizodermis or exodermis consisting of dark-colored living cells with large nuclei thick-walled (~25 µm) that show anticlinal divisions (Fig. 3C, D). The pattern of cell organization in surface tissue is the same as in *Bartsia alpina* and *Castilleja lapponica*. The primary cortex is composed of 5–6 layers in young roots and 12–14 layers in older roots of circular thin-walled actively dividing aerenchymal cells (~30–70 µm) filled with starch, and irregularly shaped air-filled cavities. The endodermis is composed of elongated dividing cells, but not always clearly expressed. The pericycle is single-layered, discontinuous and often not distinctly visible. The phloem is 3–4-layered (Fig. 3B). The xylem radius is 5–7 times larger than the thickness of the phloem ring. The primary xylem is tri- to pentarch, but more often the number of rays is not obvious. The xylem includes the conductive

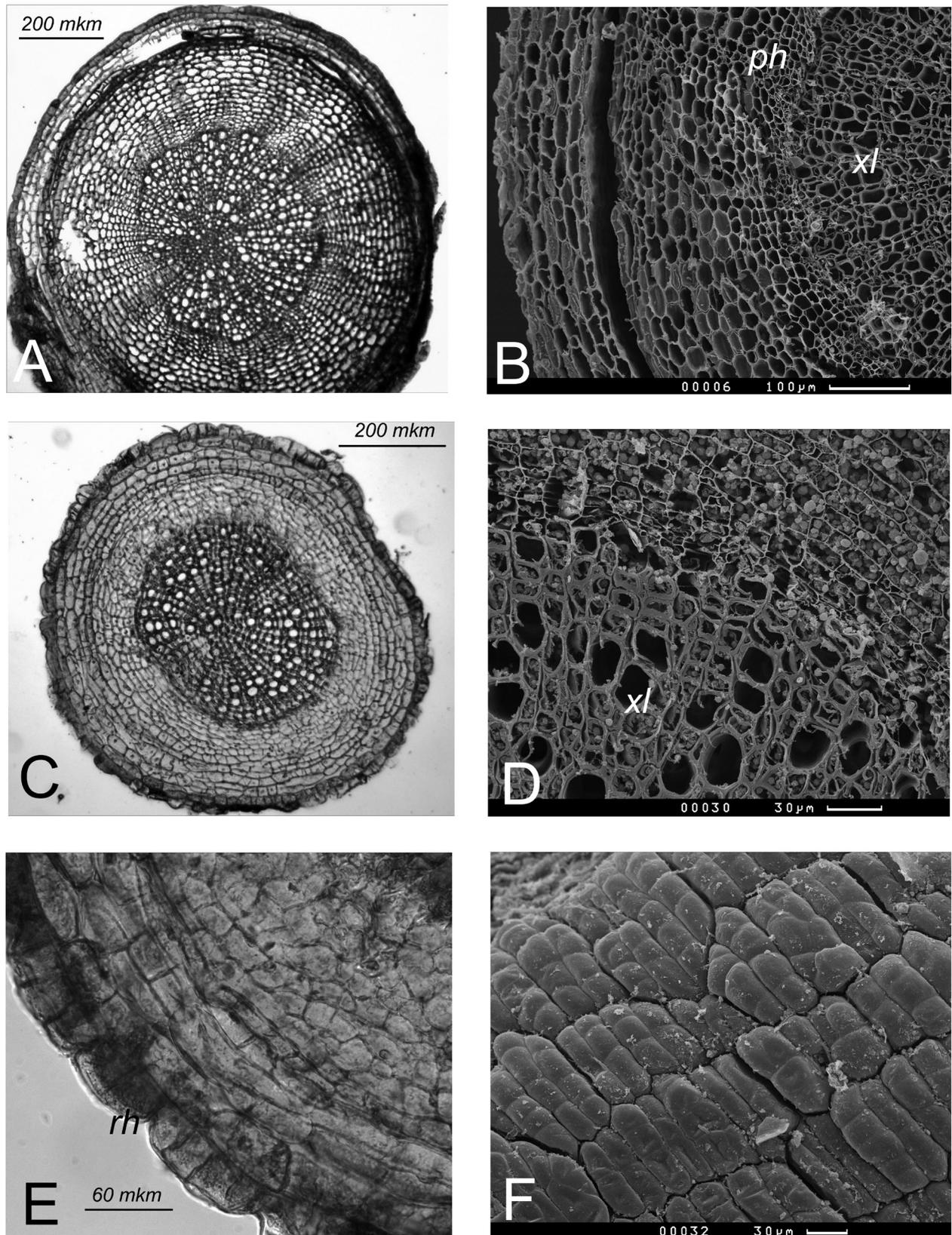


Fig. 2. Root anatomy of *Bartsia alpina* and *Castilleja lapponica*. A – cross section of *B. alpina* root; B – exodermis and cortex in *B. alpina* root (SEM); C – cross section of *C. lapponica* root; D – xylem and phloem in *C. lapponica* root (SEM); E – rhizodermis in *B. alpina* root on cross section; F – rhizodermis in *B. alpina* root, in surface view (SEM). rh – rhizodermis.

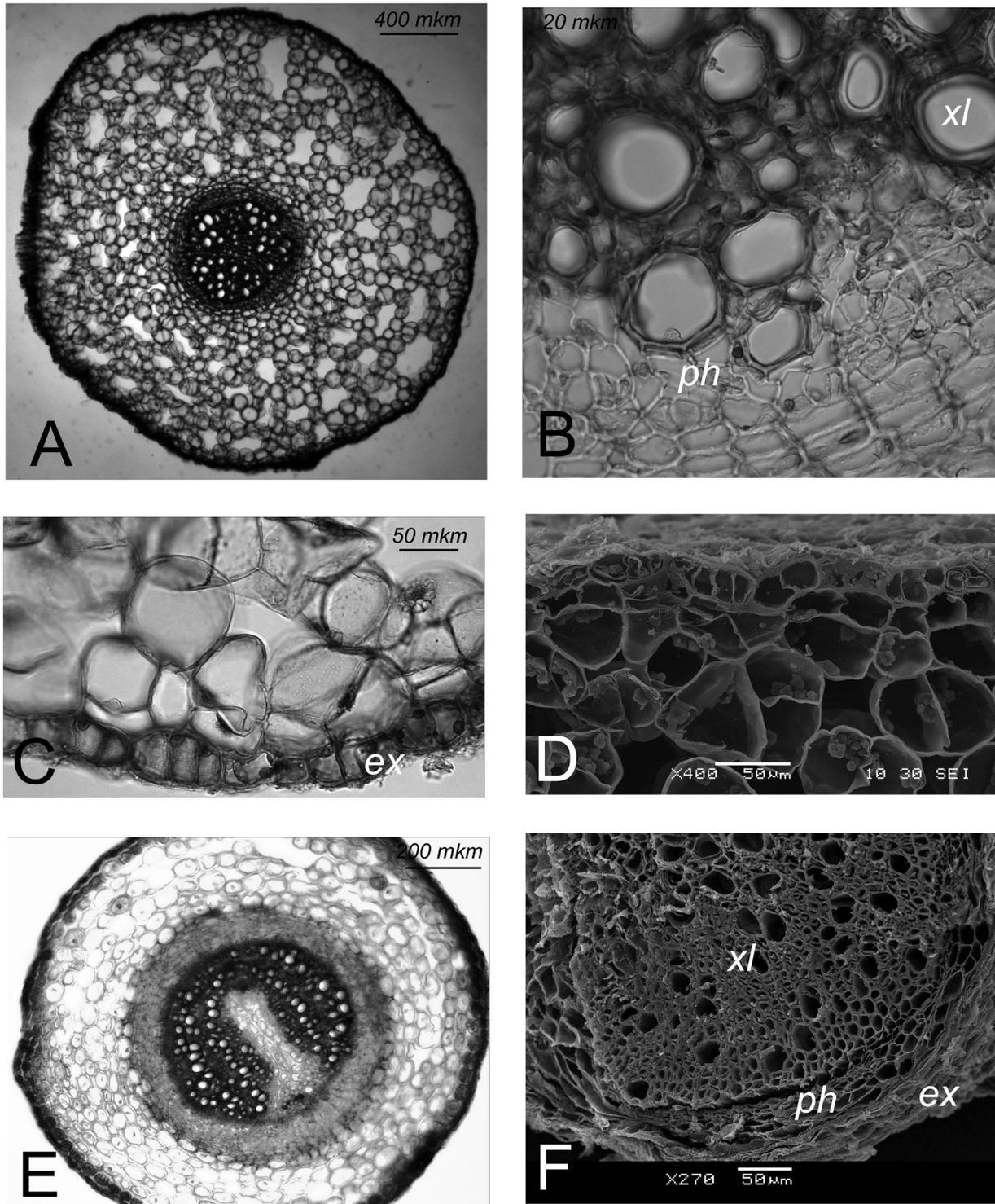


Fig. 3. Root and rhizome anatomy of *Pedicularis sceptrum-carolinum* and *Pedicularis lapponica*. A – cross section of *P. sceptrum-carolinum* root; B – xylem and phloem in *P. sceptrum-carolinum* root; C – rhizodermis in *P. sceptrum-carolinum* root on cross section; D – cortex in *P. sceptrum-carolinum* root (SEM); E – cross section of *P. lapponica* rhizome; F – cross section of *P. lapponica* root. (SEM).

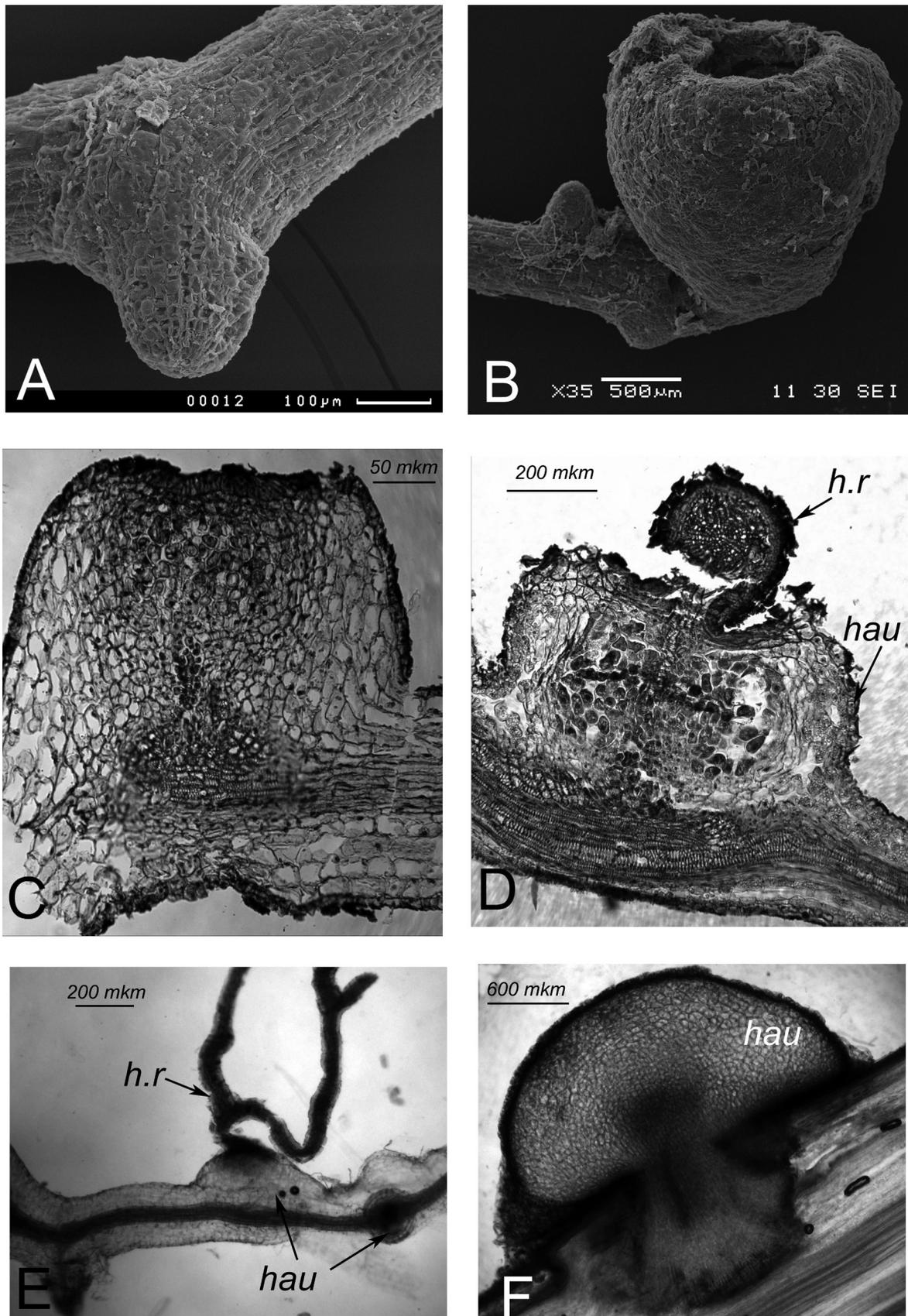


Fig. 4. Morphology and anatomy of different types of haustoria. A – blind root haustorium of *Bartsia alpina*; B – root haustorium of *Pedicularis sceptrum-carolinum*; C – cross section of blind root haustorium of *Pedicularis lapponica*; D – cross section of root haustorium of *P. sceptrum-carolinum* on the host root; E – sequential arrangement of haustorium on the root *P. sceptrum-carolinum*; F – introduction of haustorium of *P. sceptrum-carolinum* into the host root. h.r – host root, hau – haustorium.

elements (~20–50 μm) and small lignified parenchyma cells.

Adventive roots with “wart” haustorium (Fig. 4C)

At the beginning of the haustorium formation, the core of active divisions arises directly under the rhizodermis. The cells here have dark contents and thickened walls. The first division extends radially. If the root of *P. sceptrum-carolinum* contacts unsuitable surface or loses the connection with the host, the development of the haustorium stops. Such a “wart”, or “abortive” haustorium looks like a protuberance on the root with a saddle-shaped deepening

(the area of failed attachment), composed of multi-layered thick parenchyma tissue from tabular cells. The groove is composed of several layers of dark-colored crumpled suberized cells, the uppermost layer has root hairs. The internal layers of “wart” haustorium contact with the aerenchyma of the primary cortex through closely spaced parenchymal cells. In some haustoria tracheids can be seen, in such case the first can be named “abortive”.

Haustorial position and morphology

The haustorium through which the communications of hemiparasites to the subterranean parts of

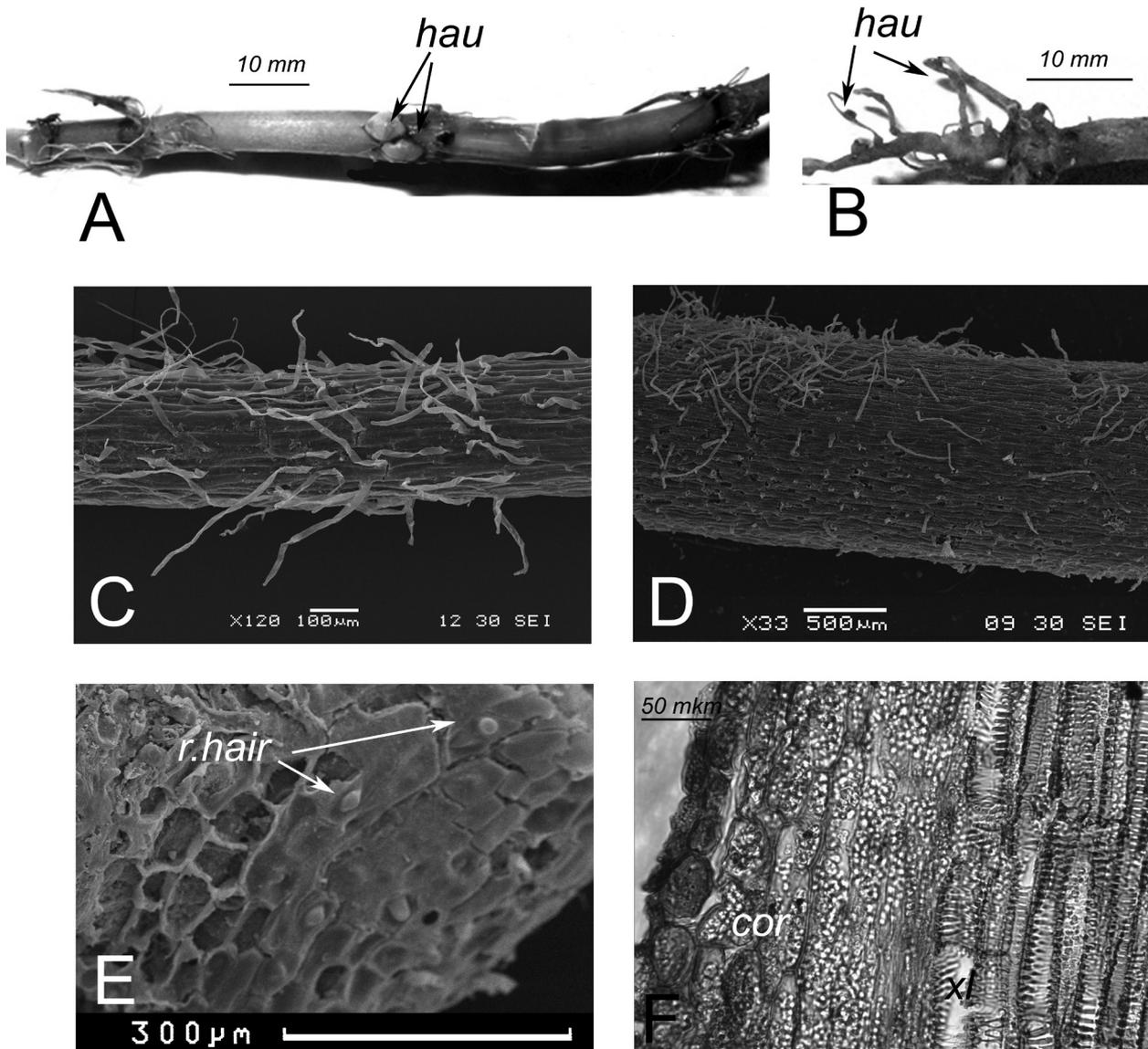


Fig. 5. Some unusual features of root and haustorium structure. A – root haustorium of *Pedicularis sceptrum-carolinum* on the rhizome of *Equisetum fluviatile*; B – root haustorium of *Rhinanthus minor*; C – root hairs on a thick root of *P. sceptrum-carolinum* in response to the presence of the host plant; D – root hairs on a thin root of *P. sceptrum-carolinum* in response to the presence of the host plant; E – the beginning of the formation of root hairs on the root of *P. sceptrum-carolinum*; F – starch deposition in the cells of the cortex and the xylem in *Rhinanthus minor* root. r.hair – root hair.

the hosts are established can develop on the primary as well as on the adventitious roots, on the thin young parts (Fig. 5C) as well as on the perennial thick parts (Fig. 5D) of the roots.

Often the haustoria of studied species are formed obviously laterally (Fig. 4A, 5B) as those of other chlorophyllous root parasites are described in the literature (Yoder, 1999). The haustoria can set close to each other in a sequential series, sometimes on opposite sides of the main axis of the root (Fig. 4E). In *P. sceptrum-carolinum* some haustoria may have an appearance of being terminal (Fig. 4B). However, in this case their apical position, as well as in many others hemiparasites, is secondary in origin. The fact is that the portion of the root that is closer to the tip beyond the haustorium can abort or remain rudimentary.

The largest haustoria were identified in *P. sceptrum-carolinum* – 0.1–2 mm in diameter and *P. lapponicum* – 0.2–2 mm in diameter. The haustoria usually vary in shape from conical to cup-shaped, from circular to elliptic (in surface view). We have found that the haustoria of studied hemiparasites can attach not only to the roots of host plants, but also their rhizomes, i.e. organs of shoot origin (Fig. 5A).

Haustral penetration and anatomy

When a parasite root is in close proximity with the host root, root hair-like structures – haustorial hairs proliferate on the haustorium rhizodermis (Fig. 5C, D, E), and at the same time, cell division and swelling occur to make a globular haustorium structure. So, the formation of haustorial hairs, which densely cover the haustorium, is one of the earliest structural events in haustorium development. The haustorial hairs are long, with a smooth surface; they usually orient towards the organ of the host plant and apparently promote the successful attachment. On further contact, hairs reduce, bearing cells that can transform to the row of parenchyma cells, closely adjoined to the root surface of the host.

The resulting layer of parenchymatous tissue excretes special enzymes (Losner-Goshen et al., 1998) that help the forming haustorium to penetrate into the host (even the lignified cells at the root of the host are not an obstacle). Then this tissue composed of small densely arranged radially elongated cells – the derivatives of the rhizodermis and underlying cells of the hemiparasites root – grows into the “cushion” fully immersed in the cortex of the host root and contacting its xylem, so called “endophyte” – that is, the haustorial part within the tissues of the host plant (Fig. 4F). Sometimes it can be seen that

the haustoria includes disparate strands that look like “search hyphae”.

At the same time or a little later some central parenchymal cells of the haustorium that retain meristematic activity (the meristematic “core”, they have dense granular content and large nuclei) differentiate into conducting elements of the xylem (Fig. 4D). The tracheal elements are nonlinear oriented spirally thickened and rather short (~5–8 μm compared with real tracheids reaching 75 μm and more in length). Tracheal elements arise not only from the deep layers of the haustorium parenchyma, but also from outer cells. When the newly formed conductive elements grow to the xylem of the host plant and are oriented perpendicular to attach to its vessels and tracheids, the effective contact hemiparasite-host is established (Fig. 4D). Phloem elements in the haustorium are not differentiated. After a successful initial contact the outer layers of the haustorium, which do not participate in the further growing inside the host body, become suberized or partially destroyed, forming a dark-colored mass on the surface.

Discussion and conclusion

The obtained data make it possible to identify some features in the root structure of hemiparasites that reflect the key stages of the transition to their special form of nutrition.

First of all, there should be noted the long existence of the primary outermost tissue of the root – the special rhizodermis that covers the entire length of both young and older roots, and constant readiness of this tissue to form special haustorial hairs, and also an unusual structure of exodermis, which in many details is similar to rhizodermis. Some researchers (Musselman, Dickison, 1975) interpret both upper cell layers as bi- or multilayered rhizodermis (= epidermis). The problem of the origin of this tissues may be solved unequivocally only through the study of the earliest stages of root morphogenesis. An important feature of the rhizodermis and the exodermis is their constant ability to divide. All these characters could be considered as the prerequisites for the rapid formation of haustoria at the first opportune moment. Indeed, one can observe many local areas along the hemiparasite roots involved in the hair development (Fig. 5D, E). The roots of the plants are in constant search of a suitable host. Recent studies (Cui et al., 2016) indicate that haustorial hairs in terms of genetic mechanisms of their inception have very much in common with the root hairs; however, the morphology and function of haustorial hairs are

distinct from those of the root hairs. Haustorial hairs serve primarily for stabilization of the host-parasite contact. They are required for efficient host interactions but not for haustorium induction by chemical signals or for the development of haustorium structures (Cui et al., 2016). Haustorial hairs play a role in maintaining physical attachment to the host surface to ensure efficient parasitism. Without the firm attachment of the haustorial hairs to a host root, the parasite roots may lose their contact and fail to form mature haustoria. It is known that root hairs appear in a special absorptive zone near the root apex, hemiparasitic hairs are not confined to belong to a specific area and, apparently, they can develop here and there along the root.

It is also important that divisions of the outer tissues play a major role in the early stages of haustorium development. In fact, the meristematic and search-stabilizing functions become quite significant for outer tissues of the roots. It is known that in the most perennial plants the outer layers of roots are represented by suberized exodermis or dead cells of the cork (phellem). There is also a question of how living outer cells of hemiparasites regulate the exchange of water and minerals. Dark content of cell protoplasts may play an important role in such regulation. The obtained data extend our understanding of the structure and functions of the rhizodermis and the exodermis.

The second important point is the structure of the vascular cylinder. Thus, the phloem in the studied plants is represented, as a rule, by a few of conductive elements: a very narrow 2-layered ring of conductive cells in *Pedicularis sceptrum-carolinum* (Fig. 3B), *P. lapponica* (Fig. 3F), discontinuous portions of conducting phloem and a thick ring of nonconductive parenchymal cells in *Bartsia alpina* (Fig. 2A, B), *Castilleja lapponica* (Fig. 2C, D).

In the xylem structure some features connected with parasitic lifestyle can be mentioned: a large amount of starch in its cells (Fig. 5F) that indicates a special type of transport and deposition of the organic substances in such plants and probably the

fuzzy location of rays of the primary xylem.

The unusual anatomy of the hemiparasites' roots often has no morphological expression except the location of haustorial hairs scattered here and there along the length of the roots. The changes in root morphology associated with a more advanced stage – the development of a haustorium itself. Once again it should be emphasized that the haustoria can be formed both on young primary and secondary thickened old parts of roots, both on the primary and adventitious roots in this case the narrow specialization of roots is not identified. It is possible that even hemiparasites' rhizomes can form haustoria as can be seen from our observations on *P. lapponica*. Very often the haustorium is “abortive”; it looks like calluses on the surface of the root. Anatomically the “abortive” haustorium consists of the parenchyma tissue, no tracheids are formed in it; the more advanced haustorium of this type can however differentiate some conductive elements. H. C. Weber (1976) considered contactless haustorium as the special types “metahaustoria” and “wart-haustoria”. We suppose that they are the normal haustoria that stopped their development or lost the contact with the host. However, it is possible that such “abortive” growths can play a special role. The root system of perennial species despite the partly parasitic lifestyle is well developed and sometimes branched as in perennial non-parasitic plants. But in case of hemiparasites the formation of a large area of root system is associated not only with functions of water absorption and protection but also with the constant search for the suitable host.

If the first contact with a host is successful, the roots of hemiparasites are modified. This process is similar in all studied species and resembles that in other hemiparasites (Dobbins, Kuijt, 1973a, b). The contact can be realized with both roots and rhizomes of the host (Fig. 5A).

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