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HISTOLOGICAL DIVERSITY OF HAUSTORIA IN SOME HEMIPARASITIC AND HOLOPARASITIC PLANT SPECIES FROM THE ROMANIAN FLORA

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Abstract: The authors investigated the origin, development and structure of haustoria in 16 hemiparasitic plant species (2 obligate and 14 facultative) and 11 holoparasitic ones (6 twiners and 5 parasitic on the roots of other flowering plants) occurring spontaneously in the Romanian flora. The present investigations emphasize that the haustoria are special organs, whose origin and structure differs from that of the roots.

Key words: histology, haustoria, hemiparasitic plants, holoparasitic plants.

Introduction

Parasitic plants have been regarded for a long time only as plants that grow and damage economically important crops, reason for why most of the existing literature deals with the methods to control these plants.

The Romanian literature is poor in morphological and anatomical studies of parasitic plants. Some morphological aspects regarding the hemiparasitic plants are found in different monographs [12], university text books and courses [10], as well as in speciality reviews [4, 5].

Morphological aspects regarding holoparasitic plants are found in the studies of Buia [3], Ungureanu and Șerbănescu-Jitariu [13], Șerbănescu-Jitariu and C. Toma [8], but none of these studies are dedicated to the haustoria in particular.

The foreign literature is quite rich regarding the morphology and anatomy of parasitic plants, but most studies deal with species not occurring in the Romanian flora.

The present authors previous papers presented the anatomy of hemiparasitic [1, 2] and holoparasitic plants [11], but the structure of haustoria was just briefly mentioned.

At some species the primary haustorium is the only connection with the host plant, at other species there are many secondary haustoria formed. The present investigations emphasize that the haustoria are special organs, whose origin and structure differ from that of the root (according to Koch, 1987); haustoria results from the inner cortex cells of both hemiparasitic and holoparasitic plant root or stem.

The development of haustoria may be independent from the host plant (*Cuscuta*), or depends on the host root exudates (*Orobanche*).

Material and Methods

In this paper the authors present the origin, development and structure of haustoria for 16 hemiparasitic species (2 obligate and 14 facultative**,** grouped in 9 genera, belonging to 3 dicotyledonous families) and 11 holoparasitic species (6 twining herbs and 5 parasitic on the roots of other flowering plants, grouped in 2 genera belonging to 2 dicotyledonous families).

The authors investigated the hemiparasitic plants belonging to the families: *Loranthaceae* (*Loranthus* - one species, *Viscum* - one species); *Santalaceae* (*Thesium* - one species) *Scrophulariaceae* (*Bartsia* - one species, *Euphrasia* - 2 species, *Melampyrum* - 5 species, *Odontites* - one species, *Pedicularis* - one species, *Rhinanthus* - 3 species). The holoparasitic plants investigated belong to the families: *Cuscutaceae* (*Cuscuta* – 6 species) and *Orobanchaceae* (*Orobanche* – 5 species).

The samples of the material subjected to analysis were fixed and preserved in 70% ethylic alcohol, subsequently transversally sectioned with a microtome and colored with ruthenium red and methylene blue. The permanent slides obtained have been photographed in “Novex” light microscope with Minolta and Canon cameras.

Results and Discussions

Obligate Hemiparasitic Plant Haustoria (*Loranthus* and *Viscum*)

The haustoria appear after the parasite contacted the host plant. Haustoria may be primary (emerged after seed germination) or secondary (which appear latter in ontogenetic development). The secondary haustoria are considered to be primitive because they appear independently of the host plant and they are the only ones in facultative hemiparasitic plants [7].

Primary haustorium of *Viscum album* has the tendency of dichotomy, but mostly only a single branch develops further and grows. The tissues of the host plant are affected by the contact with the parasite, they become hypertrophied, many of its cells being destroyed. The penetration and development of the haustoria in host plant tissues is also revealed by macroscopic longitudinal section of the parasite and host plant (Photo 1).

The structure and the penetration of haustoria are observed in the longitudinally cut micrographs. The advancement of primary haustoria does not cease when contact the xylem vessels of the host plant; they penetrate several growth rings (Photo 2). The haustoria contain many parenchymatous cells with lipid inclusions and few xylem vessels spread in the parenchymatous mass (Photo 3). The xylem vessels of the parasite present spiral and ring shaped thickenings and they are in direct contact with the host xylem vessels.

At the contact between the parasite and the host, there were observed some perturbations in the structure of the host, namely the presence of necrotized and tannin containing cells which try to isolate the haustoria. Moreover, the xylem vessels are anomalously arranged at the contact with the haustoria and the parenchymatous cells exhibit markedly thickened walls (possibly to protect the host in the place of the contact with the haustorium).

Facultative Hemiparasitic Plant Haustoria (*Thesium, Bartsia, Euphrasia, Melampyrum, Odontites, Pedicularis, Rhinanthus*)

The haustoria of the hemiparasitic plants which grow on the roots of other flowering plants develop as proliferations of cortex cells of the parasite root (exogenous). The young haustorium initially has the appearance of globular parenchymatous cell aggregate (*Melampyrum saxosum* – Fig. 1; *Pedicularis verticillata* – Photo 4). Usually, the haustorium appears circular in cross sections cut through the original root of the hemiparasite, the haustorium being longitudinally sectioned (Fig. 2). The root generating haustoria presents some modifications:

- the xylem of the stele becomes asymmetrical;
- the phloem ring and the endodermis are missing at the contact with the haustoria;
- the cells of cortex divide and form a homogeneous parenchymatous mass;
- the endodermis cells are tangentially elongate, they disappear later and the limit between cortex and stele becomes thinner;
- the belt of xylem vessels with spiral and ring shaped thickenings appears in the center of parenchymatous mass of the haustoria. The xylem vessels of the haustoria consist of elongate, parenchymatous cells at their external portion; these cells are in contact with the xylem vessels of host plant and absorb its water and minerals (*Euphrasia stricta* – Photo 5, *Melampyrum saxosum* – Photo 6). The host root becomes asymmetrical (*Rhinanthus rumelicus* – Fig. 3).

The Twining Semiparasitic Herbs Haustoria (*Cuscuta*)

Photo 1

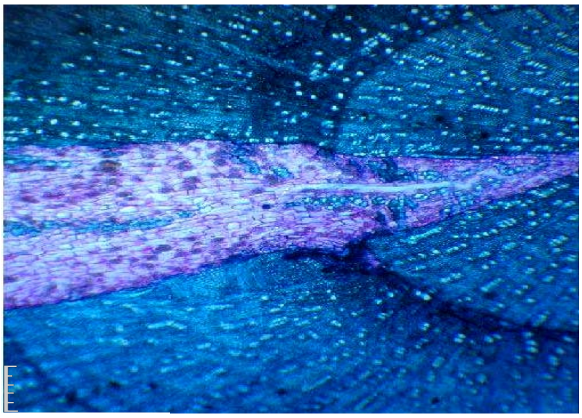

Photo 2

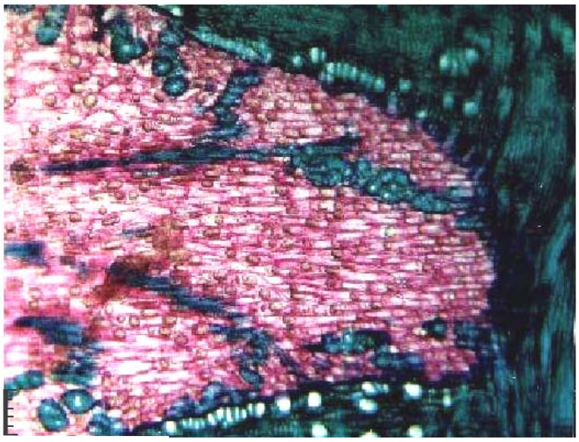

Photo 3

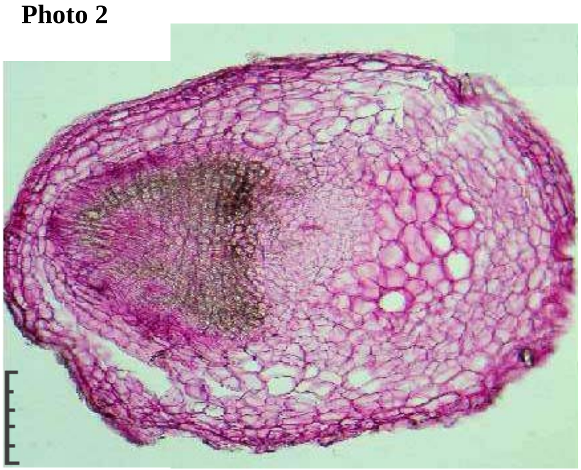

Photo 4

Photo 5

Photo 6

Photo 1: ***Viscum album*****. Haustorium (longitudinal section)**
Photo 2: ***Viscum album*****. Primary haustorium (longitudinal section)**
Photo 3: ***Viscum album.*** **Primary haustorium (longitudinal section)**
Photo 4: ***Pedicularis verticillata.*** **Haustorium (longitudinal section)**
Photo 5: ***Euphrasia stricta*****. Haustoria (longitudinal section)**
Photo 6: ***Melampyrum saxosum*****. Haustoria (longitudinal section)**

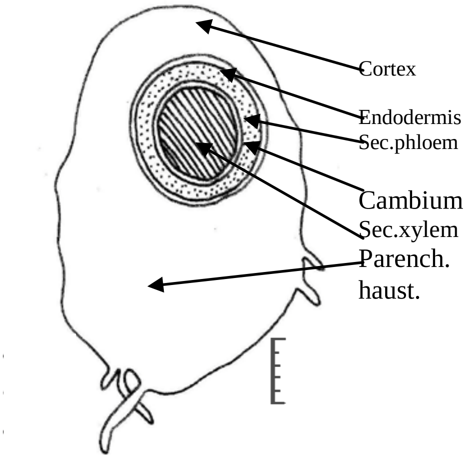

Fig. 1

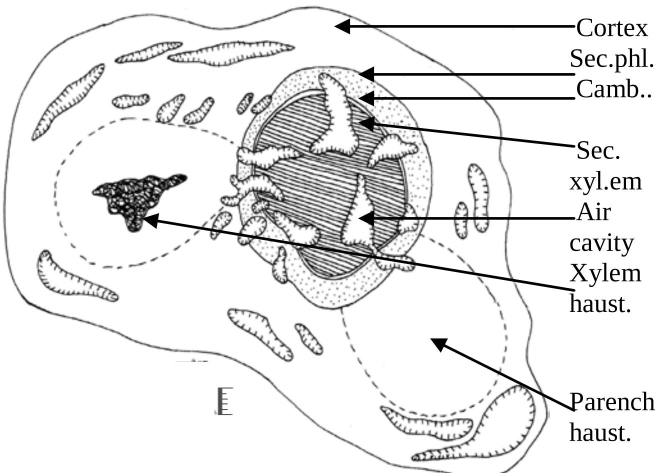

Fig. 2

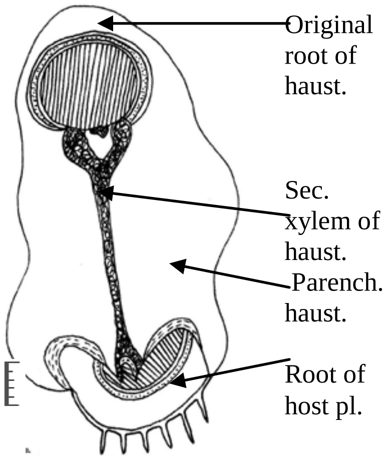

Fig. 3

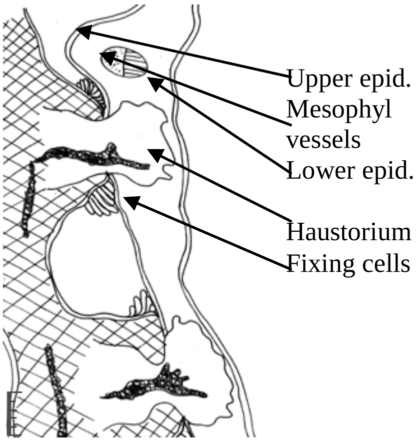

Fig. 4

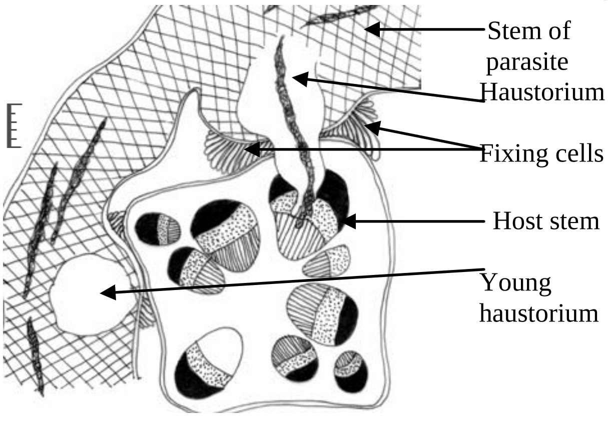

Fig. 5

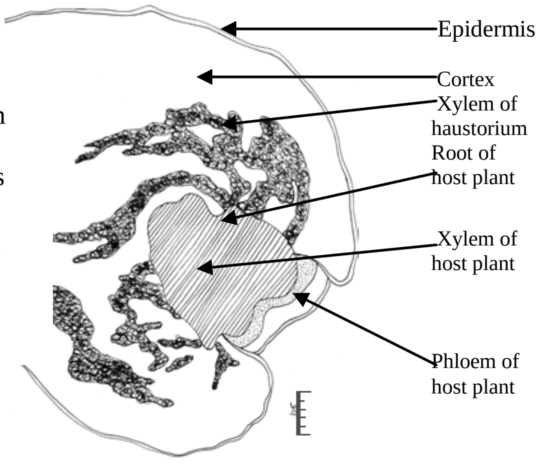

Fig. 6

Fig. 1: *Melampyrum saxosum.* Haustorium (cross section cut through the original root)
Fig. 2: *Pedicularis verticillata.* Haustorium (cross section cut through the original root)
Fig. 3: *Rhinanthus rumelicus.* Haustorium (cross section cut through the original root)
Fig. 4: *Cuscuta prodani* parasite on *Nepeta nuda* leaf (cross section)
Fig. 5: *Cuscuta epitymum* parasite on *Medicago falcata* stem (cross section)
Fig. 6: *Orobanche purpurea.* Longitudinal section cut through the haustorium

Photo 7

Photo 8

Photo 9

Photo 10

Photo 11

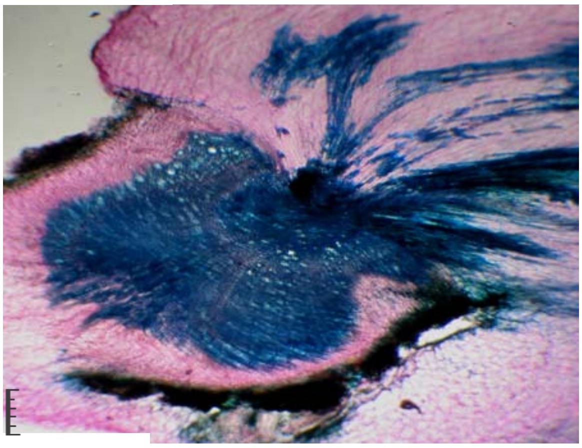

Photo 12

Photo 7: ***Cuscuta europaea.*** **Origin of the haustorium (cross section)**
Photo 8: ***Cuscuta planiflora.*** **Parasites on** ***Medicago falcata*** **stem (cross section)**
Photo 9: ***Cuscuta epilinum.*** **Parasites its own stem (cross section)**
Photo 10: ***Cuscuta prodani.*** **Parasites on** ***Rhinanthus rumelicus*** **stem (cross section)**
Photo 11: ***Orobanche arenaria.*** **Haustoria (longitudinal section)**
Photo 12: ***Orobanche purpurea.*** **The contact with the root of host plant (cross section)**

At the *Cuscuta* species the haustoria result from the proliferation of stem cortex cells.

They appear as parenchymatous aggregates of isodiametric cells and a "central cylinder" or stele with a few xylem vessels surrounded by small parenchymatous cells with moderately thickened walls, possibly transporting the organic substances (Photo 7).

The haustoria fix on different aerial organs of the host, without presenting any preference (for example *Cuscuta europaea* parasites on virgate stems of *Equisetum arvense; Cuscuta prodani* parasites on the leaves of *Nepeta nuda*) (Fig. 4). The peripheric cells of haustoria are radially elongate taking the shape of absorbent hairs and fix the parasite on the organ of host plant (Fig. 5).

The haustoria present parenchymatous mass with elongated cells which assure the contact between the vessels of the parasite and host plant (Photo 8). The stem of parasite surrounds the host organ and its haustoria penetrate the host at different levels. They may penetrate the perfascicular sclerenchyma, the phloem, the xylem and, sometimes, the pith (*Cuscuta prodani* parasites on the leaves of *Nepeta nuda*).

At some of the *Cuscuta* species *(C. epilinum, C. monogyna)*, the authors observed the phenomenon of autoparasitism (cited also by Pizzolongo for *C. pentagona*). The parasite forms haustoria which enter into its own stems when they are in close contact (Photo 9). The cells of haustoria penetrate the epidermis, cortex and stele (xylem and phloem vessels). The haustoria present belts of xylem vessels that are in contact with the xylem vessels of host stem (like in some *Cuscuta* species).

One of the *Cuscuta prodani* hosts is the hemiparasitic *Rinanthus rumelicus* which lives on other flowering plants. In this case the haustoria penetrate the host stem through the epidermis, cortex, endodermis and the cylinder of phloem vessels. The xylem vessels of parasite are in close contact with the xylem vessels of host (Photo 10).

Epirhizoide Holoparasitic Plant Haustoria (*Orobanche*)

The location of the haustoria regarding the host plant is very different and their xylem vessels exhibit different disposition in longitudinal and cross sections (Photo 11).

The structure of the haustoria is homogeneous and is represented by compact parenchyma of meatal type, with cells having cellulosic walls and a lot of starch granules inside, of various dimension and shape. The xylem vessels exhibit spiral and ring shaped thickenings, the bundles being spread all over in the parenchymatous mass; sometimes, the xylem vessels are solitary.

The phloem vascular bundles are not in contact with the xylem vessels. The ramification of the xylem vascular bundles is related to the arrangement of haustoria as regarding the host plant and the parenchymatous mass contains dense and chaotic network of xylem vessels.

The roots of host plant are asymmetrical (Photo 12) at the contact with haustoria: the phloem vessels are missing, the xylem cylinder is lobed, the external tissues are destroyed. The xylem vessels of parasite are close contact with the xylem of host plant (Fig. 6).

The parenchymatous cells located among the xylem vessels of haustoria are large, with cellulosic walls and with many starch granules.

Conclusions

The structure of haustorium in hemiparasitic plants is properly adapted to fulfill its role; it contains xylem vessels which transport the water and the minerals from the host xylem vessels to the parasite.

The hemiparasitic species investigated present haustoria consisting of parenchymatous cell aggregates, a structure which proves that the penetration into the host tissues is enzymatic and not mechanically achieved (e.g. *Viscum album* parasites on *Tilia*). The origin, development and structure of hemiparasitic plant haustorium differs from that of root, therefore haustoria can not be considered metamorphosed roots (haustoria are exogenous, not endogenous like lateral roots).

The haustoria of holoparasitic plants (e.g. *Cuscuta* species) enter into the host organs at different levels. Haustorium cells may penetrate the perifascicular sclerenchyma of the host stem, the phloem, the xylem and, rarely the pith.

The structure of haustoria in *Orobanche* species is quite simple, homogeneous parenchyma with centrally located xylem vessels. The disposition of xylem vessels is different, it may resemble the aerial stem (*O. arenaria*), or rhizome (*O. cernua*). This structure, as well as the arrangement of xylem vessels emphasizes that the haustorium is a special organ and not a root. The presence of the xylem vessels in haustoria proves that the holoparasitic plants utilize water and minerals from the host plant (observation which supplement the existing literature). In haustoria the role of phloem vessels is taken by parenchymatous cells which absorb the organic substances from the host plant.

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DIVERSITATEA HISTOLOGICĂ A HAUSTORILOR LA SPECII DE PLANTE SEMIPARAZITE ŞI HOLOPARAZITE DIN FLORA ROMÂNIEI

(Rezumat)

Autorii prezintă date referitoare la originea, modul de formare şi structura haustorilor la 16 specii de plante hemiparazite (2 obligate şi 14 facultative) şi 11 specii de plante holoparazite (6 lianoide şi 5 epirizoide) din flora spontană a României. Investigațiile noastre evidențiază faptul că haustorul este un organ special, care nu are nici aceeaşi origine şi nici aceeaşi structură cu rădăcina.