

Evolution of the secondary haustoria to a primary haustorium in the parasitic *Scrophulariaceae/Orobanchaceae*

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Abstract: In the parasitic *Scrophulariaceae* and *Orobanchaceae*, two types of contact organs exist: secondary and primary haustoria. Secondary haustoria are lateral organs, developing in large numbers and only when the seedling is fully established. In contrast, a primary haustorium represents the first developmental stage of the seedling itself. In the root system of the parasitic *Lesquereuxia syriaca* (= *Siphonostegia syriaca*) there are only secondary haustoria, but a few of them apparently develop in a terminal position. This is achieved by transferring the haustorial initiation region closer to the root apex. One can interpret this as a transformation of the apical meristem into a meristematic haustorial tissue. On the condition that an extreme shortening (abbreviation) of the primary root could happen, we discuss the transformation of the terminal secondary into a primary haustorium.

“Parasitic flowering plants penetrate with the help of contact organs, the so-called haustoria, into living host tissue in order to obtain nutrition” (WEBER 1982). This definition is essential for separating parasitic from other specialized angiosperms; they have developed and established themselves independently in many different families (KUIJT 1969). Therefore, not only parasitic plant habits (VISSER 1981) but also modes of development and biological strategies are very different. Because of this it was attempted to categorize parasitic angiosperms according to various criteria (SPERLICH 1925, OZENDA & CAPDEPON 1979). According to the place of origin of the haustorium, we have lately distinguished between root, shoot and leaf parasitism (WEBER 1980), sometimes combined in one and the same plant (WEBER 1979). In root parasitism the haustoria are root initiated (independent of whether they occur on main, lateral, or adventitious roots); in shoot parasitism the contact organs form as secondary haustoria laterally on shoot axes or terminally as primary haustoria (e.g. on the hypocotyl of the *Orobanchaceae*, RAUH 1937, KUIJT 1969, KUIJT & TOTH 1985). Secondary haustoria which develop on the seedling or later, appear to be more primitive than primary haustoria which are linked to the earliest phases of seedling development (KUIJT 1969).

If one considers the whole group of *Scrophulariaceae* and *Orobanchaceae*, one can reconstruct the phylogenetic stages of progressive parasitism (WEBER 1980). First with simply structured, lateral and secondary haustoria, later with more complex primary haustoria. In this progression an important step so far has been neglected (WEBER 1980, see Fig. 3 *c-d*): How can we explain the phylogeny from a secondary to a primary haustorium? Using the example of *Lesquereuxia syriaca*, a possible answer to this question is presented and discussed. For a more extensive report on the biology of this parasitic *Scrophulariaceae* the reader is referred to WEBER & MICKLER (1986).

Material and methods

Plants of *Lesquereuxia syriaca* BOISS. (= *Siphonostegia syriaca* BOISS. & REUT.) were investigated in their natural habitat (east of Pilion Oros near Anilion, Greece), mainly in respect to their subterranean organs, and fixed in FPA (formaldehyde, propionic acid, ethanol). The contact organs were cut with a microtome into 10 μm thick sections and embedded in Corbit-Balsam for permanent slides. Herbarium vouchers are deposited in the author's herbarium (KDM 01).

Results and discussion

Lesquereuxia syriaca BOISS. is a perennial, terrestrial root parasite with complex haustorial structures and a comparatively aggressive biology (WEBER & MICKLER 1986); this indicates a relatively advanced stage of parasitism (WEBER 1980, 1982). The numerous secondary haustoria found on the main and the lateral roots reach a diameter of up to 3 mm. The majority of these contact organs clearly is formed exogenous and laterally in the cortex below the differentiated central cylinder in the root hair zone region. This results in an interaction between parasite and host typical for the family (Figs. 1 *a*, and also 2 *a*; WEBER 1976 *b*). Particularly in later developmental stages of these organs one can often see that the formation of a haustorium can lead to the atrophication and death of the parasite root from the contact area upwards to the tip (Figs. 1 *b, c*, and also 2 *b*). In some cases this part of the parasite root, upwards of the haustorium, is not developed at all, and neither damage nor atrophication can be observed, even under high magnification (Figs. 1 *d*, and also 2 *c*): the haustorium appears to be terminal. This is confirmed by the anatomical findings on older haustoria (WEBER & MICKLER 1986).

Initiation of secondary haustoria usually occurs in the root hair zone (BAIRD & RIOPEL 1984, 1985, and also WEBER & UHLARZ 1976), i.e. exogenously by remeristemization of cortex cells (WEBER 1976 *a*). *Lesquereuxia syriaca* has no root hairs, and here the reception of a chemical stimulus from the host root must occur considerably earlier. One must conclude that the haustorial meristem is shifted towards the root tip, e.g. into the elongation zone, where the xylem differentiation has not yet started. This is confirmed by anatomical investigations (WEBER & MICKLER 1986).

Haustorial initiation in the different root parasites of *Scrophulariaceae* can occur as early as in *Lesquereuxia* or much later and in older root sections (WEBER 1982). Therefore, one can imagine a shift of this sensitive zone in different directions, and further towards the root tip, i.e. the dermatogen-calyptragen of the root apex. In such a case, the layers of initial cells would function as the haustorial meristem.

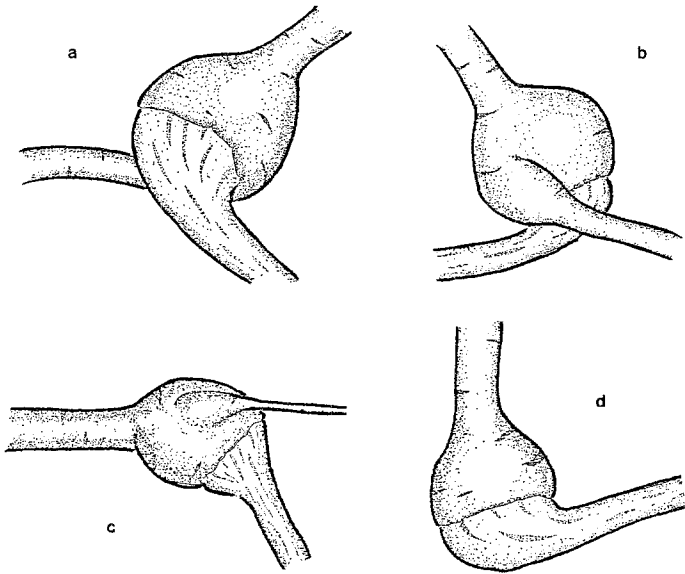


Fig. 1. *Lesquereuxia syriaca*, root initiated secondary haustoria. *a* The laterally initiated haustorium causes enlargement of the host root in the region of contact; *b* different view of *a*; *c* atrophication and *d* death of the parasite root from the haustorium towards the root tip

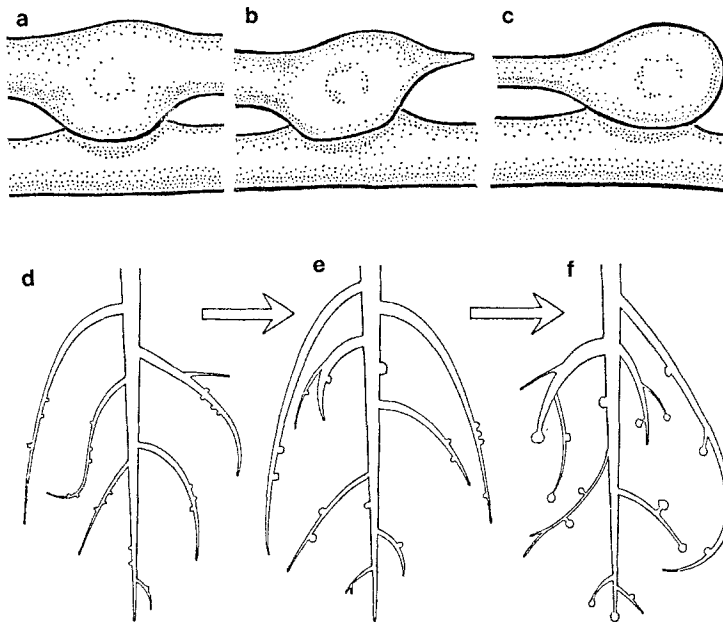


Fig. 2. *Lesquereuxia syriaca*, schematic representation of the shift of the cortical haustorial forming sensitive zone towards the root tip (*a-c*). The phylogenetic progression from simple (*d*) to structurally more complicated (*e*) lateral secondary haustoria to terminal organs (*f*) as a pre-requisite for the reduction of the root system to a primary hypocotyl haustorium

There would be no further root growth because of this now terminal secondary haustorium. Because secondary haustoria occur both on secondary and on primary roots in parasitic *Scrophulariaceae*, such a haustorium terminalisation could also occur on primary roots. Particularly because of its mode of development, such a terminal contact organ would have to be regarded as a primary haustorium. In *Orobanche*, the primary haustorium develops in a quite similar way, however at the tip of a "germ tube-like organ" (KADRY & TEWFIC 1956) and as a hypocotyl swelling (RAUH 1937).

What is the phylogenetic significance there findings for the *Rhinanthoideae* as a whole? In primitive members with a weakly developed parasitic habit, the roots are provided with numerous but hardly differentiated haustoria, e.g. in *Euphrasia* or *Odontites* (Fig. 2 d). In more advanced parasites, the formation of more efficient haustorial organs (Fig. 2 e) is linked with a greater dependence from the host, e.g. in *Pedicularis*. Due to the shift of host stimulus reception towards the root tip terminal haustoria can be formed (as in *Lesquereuxia syriaca*, Fig. 2 f). The step from this to a primary haustorium is now simple. First, the lateral roots become shorter and form, as in *Lesquereuxia*, apparently "stalked" haustoria (WEBER & MICKLER 1986); then, a similar process affects the primary root. Further reduction would lead to a short primary root with a terminal haustorium, or and finally a single hypocotyl-initiated haustorium. Such an interpretation avoids the interpretation of the primary haustorium as an organ "sui generis" (see KUIJT 1969). The primary haustorium can be regarded as a terminal secondary haustorium, which due to the extreme abbreviation of the primary root is produced directly from the hypocotyl.

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