

NOTES ON THE SEEDLING AND EARLY PRIMARY HAUSTORIUM OF *STRUTHANTHUS QUERCICOLA* (LORANTHACEAE)

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SUMMARY

The seedling of *Struthanthus quercicola* has a well-marked hypocotyl bearing raised stomata interpreted as hydathodes. The haustorial disk is already present in the seed and enlarges greatly. The development and architecture of the young haustorium corresponds closely to those of most other Santalalean haustoria, and includes a large gland, and at least two separate collapsed zones.

1. INTRODUCTION

While a certain amount of progress has been made in the study of mistletoe haustoria, the majority of species remains quite unexplored in this regard. There are indications that much variation exists and it is therefore useful to continue this exploration. The following observations on *Struthanthus* are offered in an effort to obtain a more accurate conception of the structure and, consequently, of the function of these remarkably specialized organs.

The genus *Struthanthus* (Loranthaceae) is a large, neotropical genus which has never been monographed. The material used in the present study was collected in the Talamanca Mountains south of Cartago, Costa Rica, at approximately 8000 ft., and is documented by the specimen *Kuijt 2419* (CR, UBC) as cited and illustrated under *Struthanthus quercicola* (Schlecht. & Cham.) Blume in the mistletoe revision of that country (KUIJT 1964).

In Loranthaceae two general types of haustoria are recognized. *Primary haustoria* are derived directly from the terminal, meristematic portion of the radicular apex; *secondary haustoria* are developed as lateral organs to roots other than the radicle. In *Struthanthus* both types of haustoria are present. The present study is limited to the early phases of the primary haustorium. The only previous haustorial work in *Struthanthus* has dealt with the primary and secondary haustoria when already fully established within host tissues (HEIL 1926). My general review of Santalales, including the mistletoe families, provides the framework of interpretation here accepted (KUIJT 1965).

2. RESULTS

2.1. Germination

The seed at the time of dispersal (*fig. 1*) contains two fleshy cotyledons attached nearly directly to the swollen, disk-like radicle. The cotyledons are adaxially

appressed and surrounded by a spherical body of endosperm, while the radicular disk protrudes from the latter, covered by a mass of viscous tissue (not shown). During germination all parts of the embryo enlarge, the tips of the cotyledons remaining in the endosperm until after the expanding hypocotyl has pushed the disk against the substrate (figs. 2 and 3). As soon as the tips are disengaged from the now exhausted endosperm, the cotyledons spread. The function of adherence to the host has thus been transferred completely from the viscous tissue to the young haustorial disk. The epidermal cells of the latter, in the area of host contact, grow out in a digitate fashion (figs. 6–8) to apply themselves smoothly to the host contours. The adhesive functions of these epidermal outgrowths is attested by the thin strips of bark which are often torn away from the host when the haustorial disk is removed (figs. 6 and 7).

2.2. Hypocotyl

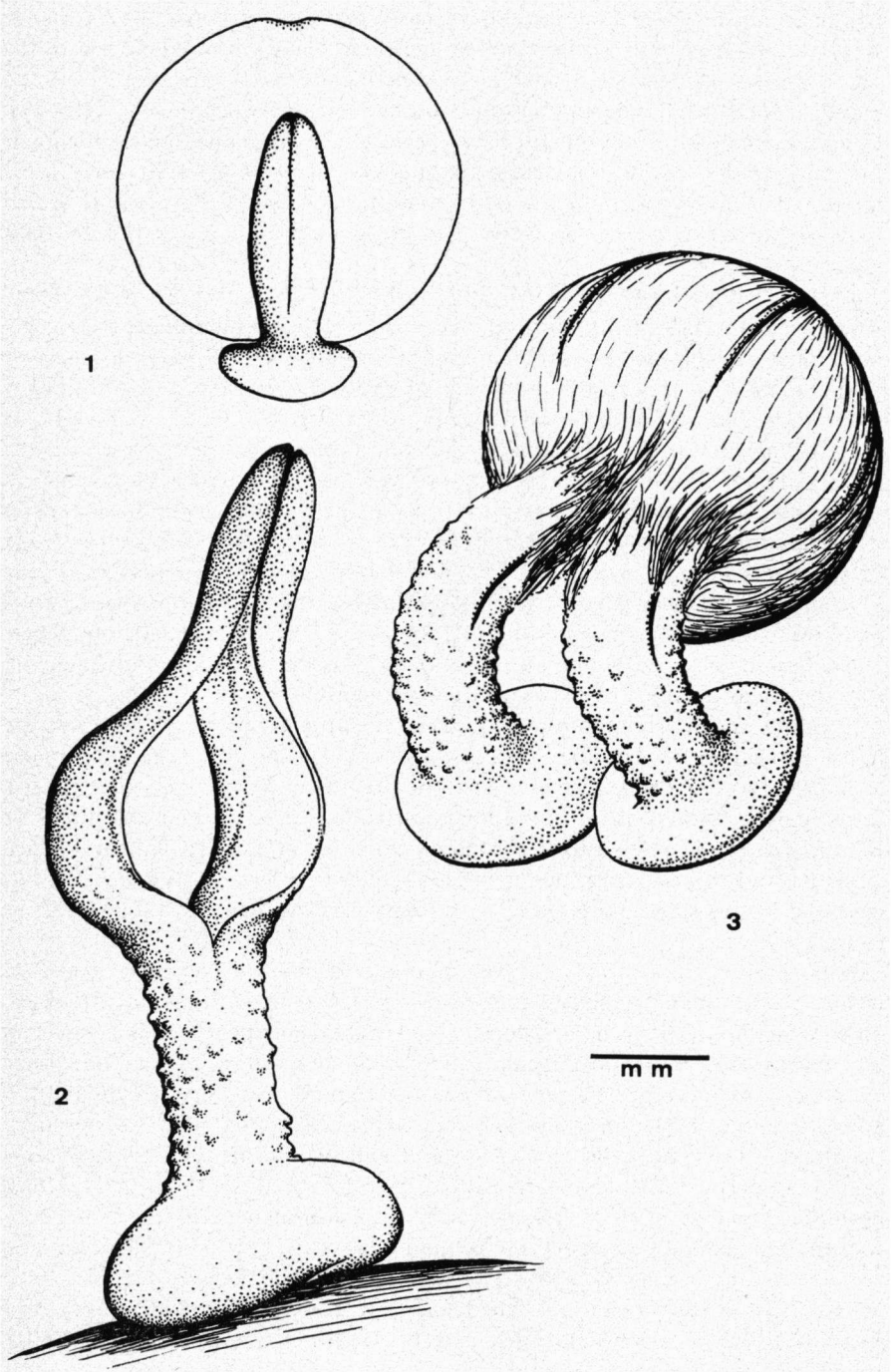
The remarkable distinctness of the mature hypocotyl in *S. quercicola*, as compared to other mistletoes, is due to the precocious formation of a haustorial disk by the radicle. The most striking aspect of the hypocotyl's differentiation during germination is the appearance of numerous epidermal protuberances (figs. 2 and 3) which are not discernable on either the cotyledons or the haustorial disk. Sectioned material shows these protuberances to have a pair of differentiated guard cells at the apex (fig. 4). A discrete substomatal chamber is present immediately below the guard cells, surrounded by parenchyma cells having few or no chloroplasts. The innermost of the latter cells may be counted to the cortex, but the outer ones evidently are part of the one-layered hypodermis which may be observed around the hypocotyl and adjacent surface of the haustorial disk. The occurrence of a substomatal chamber is rather striking in an otherwise very compact organ. The combination of guard cells, substomatal chamber, and subjacent modified parenchyma suggests a hydathodal function, and the papillae are tentatively designated as such. Although hydathodes are often thought of as vasculated structures, this is not invariably so, as attested by those of two other parasites, *Cuscuta* and *Euphrasia* (RENNER 1934; SEEGER 1910).

The hypocotyls or radicles of several other mistletoes bear papillar structures, but not all of these may be comparable to the present ones. *Phrygilanthus aphyllus* (Miers) Eichl. has multicellular papillae on both the hypocotyl and the haustorial disk itself, those on the disk possibly serving to stabilize the seedling during germination (REICHE 1904). No structural features indicate a hydathodal function. *P. tetrandrus* (Ruiz & Pavon) Eichl. has similar papillae (REICHE 1907). In both of these species the papillae differentiate before the seed is disseminated. The cultured seedlings of *Amyema* and *Amylothea* may produce very striking

Fig. 1. Longitudinal section of mature seed of *S. quercicola*, the viscous tissues removed, showing the haustorial disk situated outside the spherical endosperm.

Fig. 2. A seedling just after the cotyledonary tips have withdrawn from the endosperm, the haustorial disk attached to the substrate.

Fig. 3. A rare diembryonic seed, showing curved hypocotyls and cotyledons, and haustorial disks being applied to the substrate.



papillae some of which have developed buds under certain conditions (JOHRI & BAJAJ 1964). It is unfortunate that no anatomical work has been done in the above genera, so that we do not know whether stomata were present on the papillae. The stem tubercles in mistletoe-related Myzodendraceae (HOOKER 1846) are accompanied by a pair of guard cells and a large substomatal chamber, but are far more complex than the hydathodes of *Struthanthus*. It is also of some interest that in Myzodendraceae (JOHNSON 1889) and several species of *Arceuthobium* and *Phoradendron* (KUIJT 1960) stomata are present on the radicle itself.

2.3. Anatomy of the early primary haustorium

The haustorial disk in the early phases of the seedling's germination is nearly hemispherical, the convex surface pointing forward (*fig. 5*). As in most other mistletoe radicles, there is never any sign of a root cap. Instead, a discrete small-celled tunica and epidermis is continuous around the disk and the remainder of the seedling. Below this "epidermis" a second layer is discernable especially in the hypocotyl, by its weaker absorption of stains as compared with the cortical tissues below. The entire convex portion of the disk is apparently in a meristematic condition. From the hypocotyl, two provascular strands are seen to reach down into the center of the disk. A few tracheary elements are present on the adaxial side of these strands. The full hypocotyl probably has four such strands as is the case in *Phthirusa pyrifolia* (HBK) Eichl., a related mistletoe (KUIJT 1969, *figs. 2-27*). The hydathodes are already differentiating as indicated by slightly raised portions of the hypocotylar epidermis.

The subsequent growth of the disk, especially after contact with the substrate has been made, leads to a flattening of the convex distal surface, and eventually a rounding of the flanks (*figs. 6 and 7*). The mature haustorial disk, therefore, is once again a hemispherical body, but the convex surface is now the upper or proximal surface. The superficial cells in portions of the attachment surface elongate and appear to apply themselves to the substrate. When a disk is removed at this stage, thin layers of the superficial host tissues usually adhere to it.

Meanwhile significant histological changes within the haustorial disk are initiated. Meristematic activity appears to shift away from the periphery of the disk. More importantly, the haustorial gland makes its appearance. *Fig. 6* shows an elliptical area in the most distal portion of the disk where cells have lost their staining characteristics. This area, known as the gland, consists of an apparently autolytic tissue developed from the meristematic cells of that area. Surrounding the gland is a lining of cells which also seem to be in various stages of deterioration. It is particularly important with respect to the interpretation of future developments that we note the concentration of meristematic tissue in the central area immediately proximal to the gland (*fig. 6*). There is no suggestion as yet of a collapsed zone.

The gland of the haustoria of mistletoes and their relatives is an elusive and puzzling tissue, a resumé of which may be found in an earlier article (KUIJT 1965). It has been reported for only a few mistletoes so far. In all except the pre-

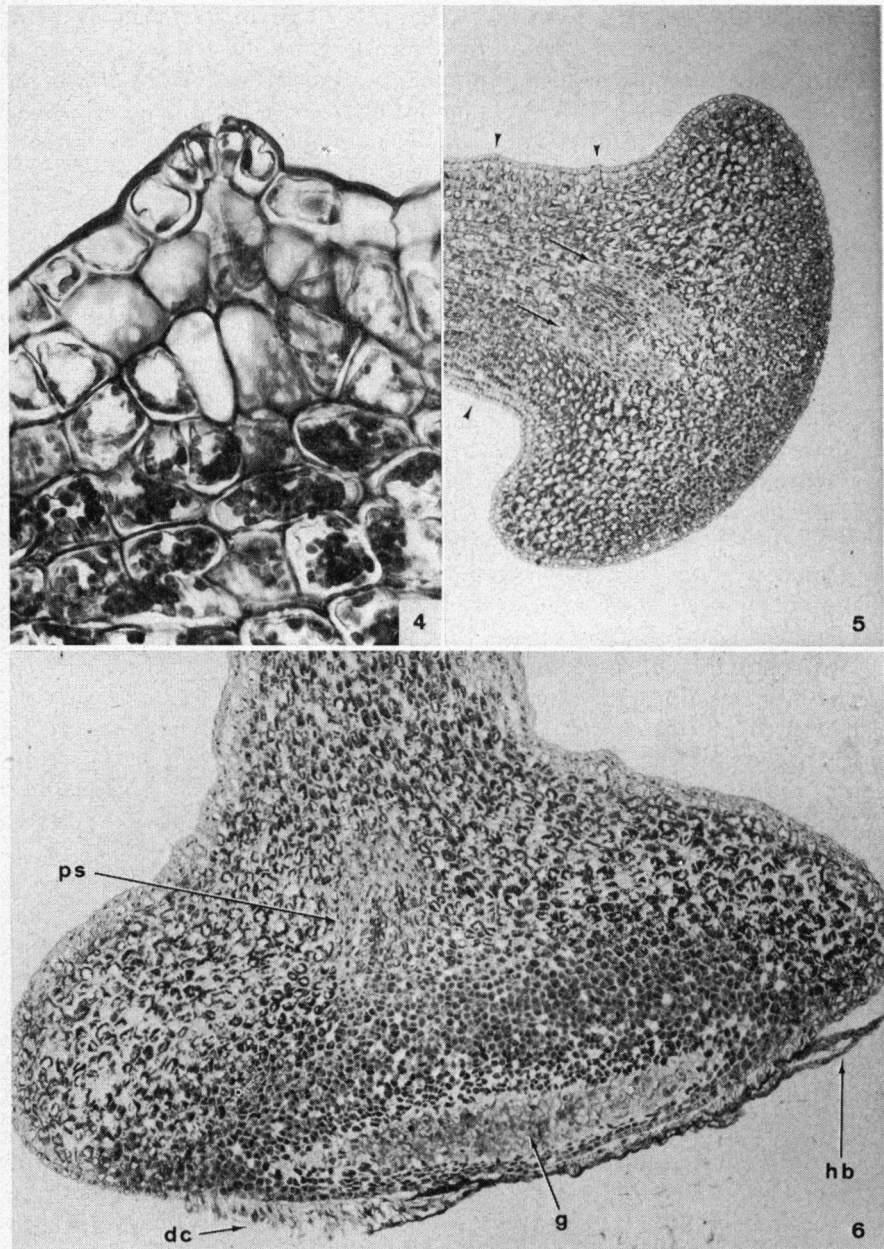


Fig. 4. Section of hydathode on hypocotyl. $\times 275$.

Fig. 5. Longitudinal section of young haustorial disk at an early stage of germination. Small arrows: differentiating hydathodes; large arrows: provascular strands. $\times 50$.

Fig. 6. Longitudinal section of haustorial disk with gland (g) at maximum development. ps = provascular strands; dc = digitate cells of epidermis; hb = host bark. $\times 52$.

sent report, *Psittacanthus allenii*, and *Phrygilanthus heterophyllus* (KUIJT 1970; REICHE 1907) the mistletoe gland, where mentioned or illustrated, has been in secondary haustoria. As pointed out in the above-mentioned review article, the infrequency of such reports may be misleading as the gland may well be an evanescent feature in many cases. A detailed developmental study has not been published for any of the haustoria reportedly producing a gland.

Fig. 7 shows the internal organization at the time (probably the second time) that invasion of the host is attempted. The massive flanks of the disk, made up of relatively undifferentiated parenchyma enclosed by an epidermis and hypodermal layer, surround a structurally complex inner region requiring a number of comments.

The largely provascular strands (faintly visible in *fig. 7*) which lead from the hypocotyl are essentially unchanged from the time of germination. An interesting addition, however, is the differentiation of short vessel members in an interrupted and irregular plate-like formation across the central portion of the disk, just above the outer collapsed zone. The cells directly below these vessel members are dividing actively in a plane more or less perpendicular to the hypocotylar strands. These irregular transverse vascular strands are continuous with the hypocotylar ones and may be comparable to the much more elaborate vascular proliferation in the primary haustorium of *Loranthus europaeus* Jacq. (KUIJT 1969, figs. 2-26a).

Two concentric collapsed zones are visible (*fig. 7*, arrows). The outer one reaches from just below the vascular "plate" into the lower periphery of the disk. The inner collapsed zone does not extend into this periphery but may be traced nearly to the tip of the massive wedge-like protrusion occupying the axial portion of the attachment surface. From near the vascular "plate" a tongue-like intrusive organ reaches out to the host surface. Its terminal portion is clearly meristematic in nature and has left behind long files of cells. Immediately ahead of it is an extremely dark-staining tissue which seems to be on the verge of collapse (*fig. 8*). I am not certain whether these elongated cells are, or have been, part of the intrusive organ (with a function comparable to that of a normal root cap) or whether they are "resident" cells being crushed by the advancing intrusive organ. The intergradation between "crushed" and meristematic cells, and the fact that an aperture has already been forced in the superficial disk-tissues, appears to support the former interpretation.

The structure of the early primary haustorium of *Struthanthus quercicola*, therefore, seems to conform to my earlier (KUIJT 1965) interpretation of the Santalalean haustorium. An endogenous, intrusive organ originates above the gland and grows forward through the glandular cavity and superficial disk tissue to reach the host surface. It leaves a zone of crushed cells in its wake, called the inner zone of collapsed cells in the foregoing description, as an indication of the channel of its passage through the gland. The outer zone of collapsed cells appears to have a different origin and, in fact, may well be formed earlier than or at the same time as the young intrusive organ.

In *fig. 7* the tissues axial to the inner collapsed zone are thus regarded as con-

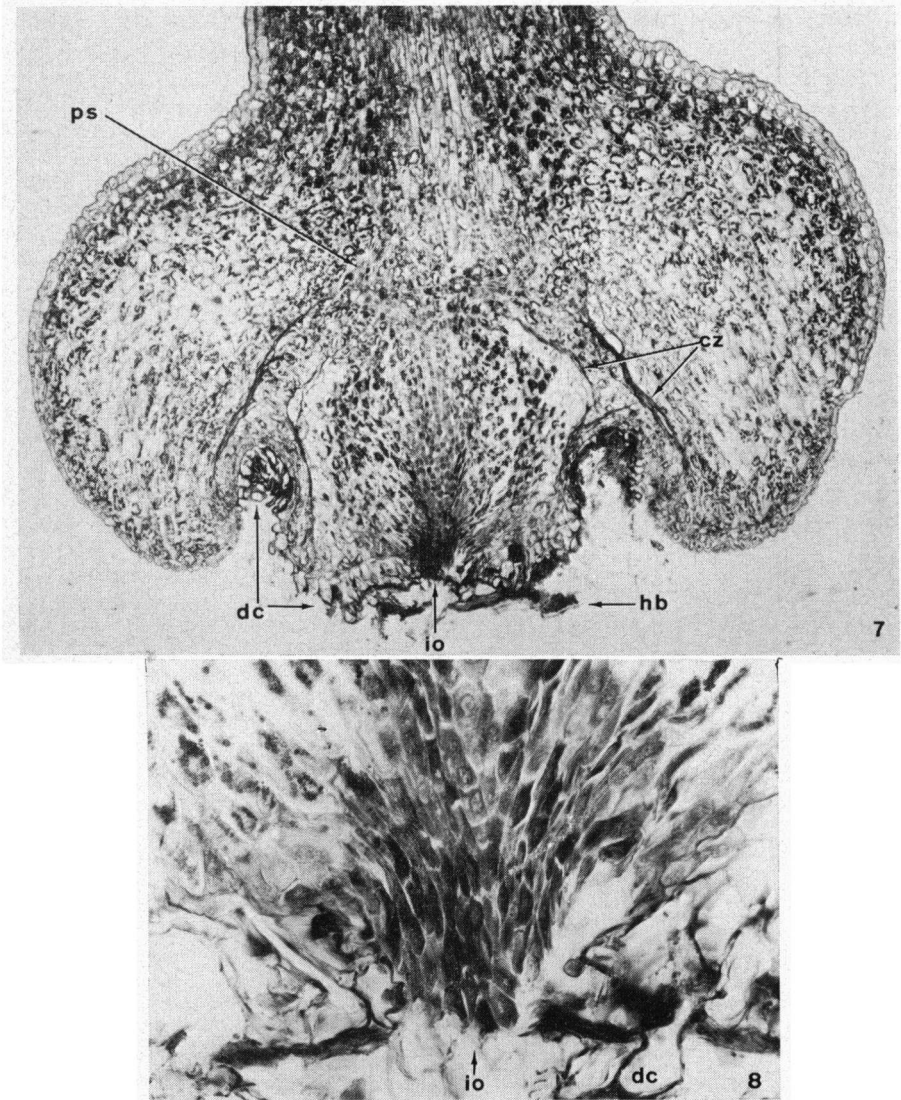


Fig. 7 and 8. Longitudinal section of a mature haustorial disk at the time of host entry. Fig. 7, $\times 52$; Fig. 8, tip of intrusive organ enlarged, $\times 240$. cz = collapsed zones; dc = digitate cells of epidermis; hb = host bark; io = intrusive organ; ps = provascular strand.

stituting the original intrusive organ which failed to effect entry into the host and subsequently flattened out to form a new adhesive surface, again with somewhat columnar superficial cells. The bulk of the earlier adhesive cells can be recognized in the bays situated between the inner and outer collapsed zones. A second intrusive organ, originating within the first, is moving forward for a renewed effort. It should be mentioned that there is no clear evidence of a new gland associated with the second intrusive organ, although some of the cells immediately surrounding the latter might be interpreted as its peripheral remnant.

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