

ON THE NATURE AND ACTION OF THE
SANTALALEAN HAUSTORIUM, AS EXEMPLIFIED
BY PHTHIRUSA AND ANTIDAPHNE
(LORANTHACEAE)

JOB KUIJT

(*Department of Botany, University of British Columbia, Vancouver, Canada*)

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ABSTRACT

The original intent of the present study was an inquiry into the architecture of the secondary haustoria of the mistletoes *Antidaphne viscoidea* and *Phthirusa pyrifolia*, each representing one of the two subfamilies of *Loranthaceae*. In the course of this study it has become clear that there are fundamental similarities uniting the haustoria of the entire order, *Santalales*. The need for integration of all knowledge of Santalalean haustoria became more pressing as the work proceeded and has culminated in this article in its present form. This work, then, represents an integrated review of the structure and mechanism of Santalalean haustoria, introduced by an account of the haustoria of *Phthirusa* and *Antidaphne*.

PHTHIRUSA AND ANTIDAPHNE

The mistletoe haustorium of the temperate zones is a direct outgrowth of the radicular apex of the seedling. Even such complex absorptive systems as those of *Arceuthobium*, *Phrygilanthus aphyllus*, and some species of *Phoradendron* can be traced back to their origin from the apical meristem of the primary root. In a large number of tropical and some subtropical *Loranthaceae*, however, secondary roots are formed from the base of the plant or from branches. Such roots are known as *epicortical roots*, and follow the branches of the host, producing secondary haustoria at irregular intervals. Secondary haustoria, partly through their limited geographic occurrence, have received little attention from anatomists. The present account of the young secondary haustoria of *Phthirusa pyrifolia* (HBK.) Eichl. and *Antidaphne viscoidea* Poepp. and Endl. demonstrates not only the potential systematic importance, but also the unexpected complexity of some of these haustoria.

The mistletoes here studied are representatives of the two subfamilies of *Loranthaceae*. *Phthirusa pyrifolia* is a member of subfamily *Loranthoideae*. It is impossible to say, at this time, whether *Phthirusa* occupies a primitive or advanced station within the subfamily. As pointed out elsewhere, however, the most primitive *Loranthoideae* almost certainly are *Atkinsonia*, *Gaiadendron*, and *Nuytsia* (KUIJT, 1965). The material of *Phthirusa pyrifolia* in this study is traceable to plants growing on *Codiaeum* in San José, Costa Rica (KUIJT 2425 as reported in KUIJT, 1964b). In the University greenhouses at Vancouver I have been able to grow the species to maturity from seed imported in August, 1962.

The plants are growing on *Tibouchina*, *Nerium*, and *Codiaeum* and are producing viable seeds. The *Phthirusa* materials in this study are obtained from these greenhouses. (Illustrations of epicortical roots of this species may also be seen in KUIJT, 1964a, fig. 8, d and f.)

Antidaphne was not known to possess epicortical roots at all until this fact was recently demonstrated (KUIJT, o.c.). The uniqueness of its epicortical roots is that they are evanescent features. A mature plant of *Antidaphne* has no surviving epicortical roots. *Antidaphne* is one of a few contenders for the most primitive position in subfamily *Viscoideae*. Materials used in this study were also collected in Costa Rica, and correspond to my collection no. 2433 as cited and illustrated in the above-mentioned monograph.

As secondary haustoria are lateral outgrowths of epicortical roots, it behooves us to take a casual glance at the structure of these organs. (I am leaving out of consideration here the secondary roots of *Atkinsonia*, *Gaiadendron*, and *Nuytsia*.) The material at my disposal here does not belong to either *Antidaphne* or *Phthirusa* but rather to *Struthanthus marginatus* (see the Costa Rican monograph) collected from a leguminous tree on the University campus at San José, Costa Rica, in 1962. The root apex of *Phthirusa* probably is not significantly different from that of *Struthanthus*; the two genera are extremely close taxonomically and have, upon occasion, been united.

Notwithstanding the terminology of certain authors (EICHLER, 1868: *bdallorhizae*; SOLMS-LAUBACH, 1877; *rhizoids*) there can be no doubt as to the morphological status of the epicortical roots. They are nonarticulated, leafless, clearly endogenous in origin and exarch in vascular development. Furthermore, they possess a small but recognizable rootcap, notwithstanding THODAY's (1960), REICHE's (1907), KARSTEN's (1852), and KOERNICKE's (1908) statements to the contrary.

Median sections of epicortical root apices of *Struthanthus marginatus* from Costa Rica show an organization identical to that illustrated by HEIL (1926, Fig. 9) for *S. quercicola*. The apex and adjacent portions of the root are covered by an irregular layer of 1-3 cells in thickness, the cells of which are greatly enlarged. It is quite clear that this cap-like layer is derived from a concentric system of sub-dermal cells reminiscent of a cork cambium. The outer cells are dead and partially disintegrated. Nothing comparable to root hairs is present. An indistinctly delimited group of internal cells represents the meristematic center. Vascular differentiation takes place surprisingly close to the apex. An analysis of apical organization cannot be provided at this time, partly because of the sluggish growth and consequent rarity of mitoses in epicortical roots. At any rate, the apical meristem in *Struthanthus* (and almost surely in *Phthirusa*) is undoubtedly internal, and not a superficial one. Essentially the same findings are reported elsewhere for *Loranthus micranthus* (MENZIES, 1954) and again for *Struthanthus* (GOEBEL, 1932). It should be added that in Menzies' *Loranthus micranthus* and, more strikingly, in *Antidaphne viscoidea* (Fig. 8), dead cells are disengaged from the root cap in discrete patches. These patches remain attached at the end nearest the cap, and become up-

lifted on the other end, giving the root a peculiar scaly appearance.

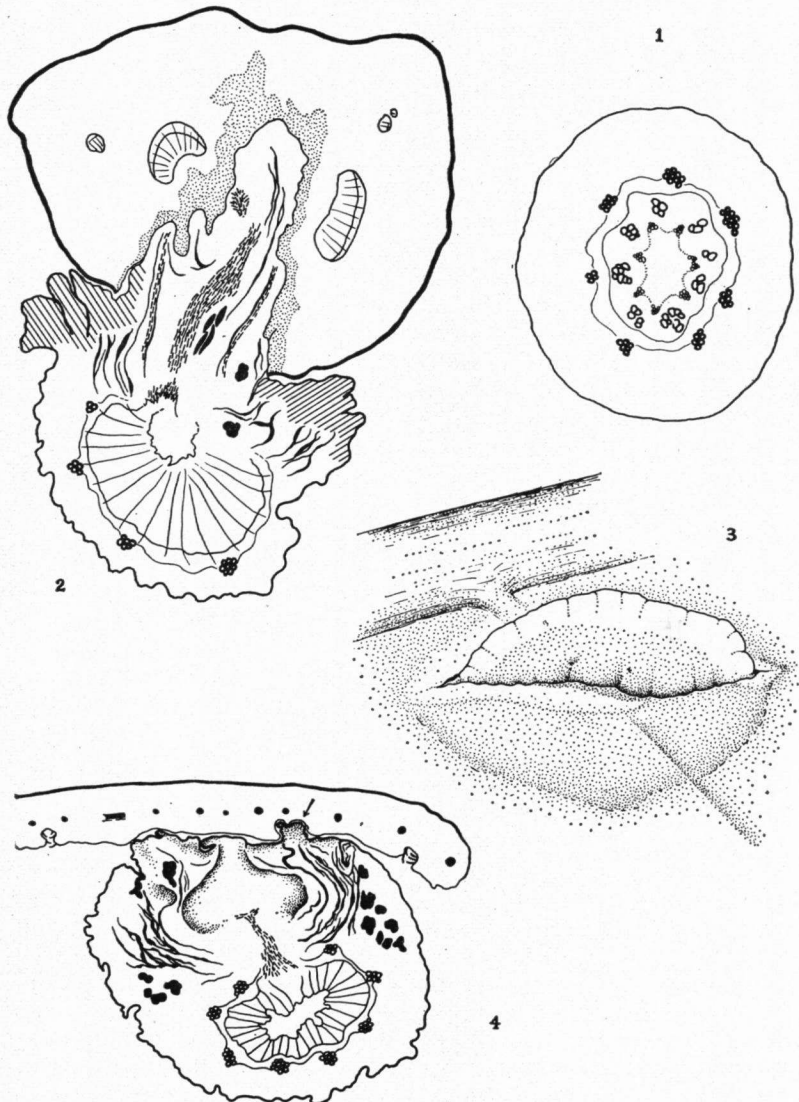
It must not be thought, however, that epicortical roots are typical roots in all respects. They are much more massive than ordinary dicotyledonous roots and are, in fact, very similar in appearance to the clinging roots of many epiphytic aroids. There is no sign of root hairs anywhere along the root. Internally, the most unusual feature is the presence of a well developed pith, at least in the vicinity of haustoria. Secondary xylem and phloem are initiated at an early stage; phloic fibers in about 8 groups are present in *Phthirusa* but in *Antidaphne* soon form a somewhat interrupted cylinder. THODAY (1960) reports other unusual details for *Dendrophthoe falcata* which are reflected in those presented below for *Antidaphne* and *Phthirusa*.

A peripheral point of interest here is the fact that, in contrast to epicortical roots, the primary root at the time of germination is quite devoid of root cap. The radicular apex is covered by a single superficial tunica layer. This is known to be true for *Antidaphne* and *Phthirusa* as a result of the present work; for *Viscum album* (THODAY, 1951), *Arceuthobium* (KUIJT, 1960), *Korthalsella* (STEVENSON, 1934), *Phrygilanthus celastroides* (McLUCKIE, 1932), *Dendrophthoe falcata* (Singh, 1954), and *Tupeia* (SMART, 1952). Since this list represents quite a random selection, we can probably be certain that all mistletoes which develop a terminal radicular haustorium—i.e., all except *Atkinsonia*, *Nuytsia*, and *Gaiadendron* (KUIJT, 1965)—have a tunicate root meristem. Looking beyond the *Santalales* for a moment to such families as *Lennoaceae*, *Krameriaceae* and even *Orobanchaceae*, and considering the need, for living, possibly digestive cells at the tip of the intrusive organ, it would seem that a terminal haustorium of necessity must be tunicate, or at least without massive root cap.

PHTHIRUSA PYRIFOLIA

The epicortical roots of *Phthirusa pyrifolia* are greenish, blunt organs, 1–2 mm in diameter when young, and clinging rigidly to the host surface (Figs. 14–16). They adapt themselves to host contours to a remarkable degree. Ordinarily almost the entire ventral surface of the root is in contact with the host and appears to be cemented to it. This contact is later broken near haustoria through local expansion of the haustoria and the host branch. A number of pustule-like lenticels are present on the root, sometimes forming short, interrupted longitudinal series.

In transection a *Phthirusa* root, taken some distance away from a haustorium, shows 6–8 rather indistinct protoxylem points (Fig. 1). Many cells between, and interior to the protoxylem groups have become lignified and may be regarded as metaxylem. Metaxylem differentiation may stop short of completion, thus leaving some irregularly spaced parenchyma cells. The latter are probably continuous with the large pith which is in evidence in the vicinity of haustoria. Alternating with the protoxylem groups are small groups of vessel members perhaps indicating the beginning of secondary growth. Indeed, at this



Figs. 1-4. *Phthirusa pyrifolia* on *Nerium oleander*, University Greenhouses, Vancouver.

1. Transsection of young epicortical root, showing pith surrounded by concentric layers of xylem and phloem, the latter with 7 groups of fibers. ($\times 50$)
2. Transsection of secondary haustorium invading petiole. Stippled area of host, and hatched area of parasite necrotic. The intrusive organ has axial as well as some peripheral xylem (broken lines). Collapsed layers (solid lines) visible in both internal and external haustorial portions. Sclerenchyma in black. ($\times 25$)
3. Crest of secondary haustorium emerging from upper epidermis of host leaf. ($\times 50$)
4. Young secondary haustorium formed on lower surface of host leaf. Stippled area around parenchymatous core represents the purple tissue referred to in text; for other tissues, see under Fig. 2. Note also invasion of stomatal crypt of host leaf (arrow).

time, a nearly continuous cambium can be traced out, surrounded by a thin layer of phloem. Each group of vessel members is matched, across the cambium, by a group of thick-walled fibers in the outer phloem; these fibers correspond in position to the protophloem from which they may well be derived. A thin cork layer envelops the entire root. No other sclerenchyma is in evidence.

Study of several mature plants has not brought forth any recognizable pattern of haustorial distribution. It seems indicated on the one hand that haustoria are initiated much further from the root apex than in such parasites as *Gaiadendron* (Куйт, 1963) or *Santalaceae*. This appearance may be due, however, to the obscurity of the young haustoria. At any rate, it is common to find the youngest 10 cm of a root to be without visible haustoria. On the other hand, it is clear that older root portions (certainly those proximal to existing haustoria) have lost the ability to form haustoria.

Near the base of the plant, haustoria are usually spaced about 3 cm apart. Further outward the spaces become somewhat larger, even up to 10 cm. Any regularity present is obscured by aborting root tips and occasional branching.

We can, therefore, not identify the mechanism which determines the position of haustoria. Gravity and light are not recognizably involved. A thigmotropic response can probably also be ruled out, since the entire young root is in contact with the host, and since prominent ridges on the host do not appear to be favored by haustoria. Beyond these negative statements, unfortunately, nothing positive can be added.

The formation of haustoria in *Phthirusa* is an exceedingly inconspicuous process. Unlike the haustoria of many other Santalalean parasites, a mantle is not recognizable externally. A slight swelling of the root is all that is normally visible. Since the entire root adheres closely to the host surface a young haustorium is impossible to spot with any degree of certainty.

Occasionally the resistance met by the intruding organ is prohibitive, or adhesion to the host surface is insufficient. The result is that the root is forced up somewhat by the growing haustorial organ. A certain amount of root curvature may then take place (Fig. 6) forcing the haustorium toward the host, but even this effort sometimes fails, and the freely suspended intrusive organ can be studied to advantage. In other instances the epicortical root may grow along the lower surface of a host leaf, one or more haustoria entering the leaf. Such leaf-parasitic haustoria are illuminating as they quickly pass through the leaf, the entire intrusive organ emerging on the upper surface (Fig. 3), thus affording a unique opportunity of study. These two types of haustoria, externally as well as anatomically, allow us a reasonably accurate interpretation of secondary haustoria in *Phthirusa*.

It is clear from my observations that the intrusive portion of the haustorium is not a peg-shaped organ, as has often been supposed in other mistletoes. Instead, it is a wedge or crest of parenchymatous tissue which emerges from the interior tissues of the root. It is this arching

crest which attempts to enter the host organ by means of a mechanism which is as yet uncertain. The net effect of such a successful "sucker" is to slice through host tissues. This is clearly evident in Fig. 3 where a secondary leaf vein has been severed, apparently without the least difficulty.

One gets the impression from haustoria such as that in Figs. 3, 5 and 6 that an endogenous haustorial crest is formed not just once, but several times in succession, younger crests emerging from the inner tissues of older ones. This appearance will be confirmed below by means of anatomical details. We find in such cases a series of crests, the older ones near the base forming collars around the younger ones. The youngest crest is lightest in color and often papillose and of irregular contours, somewhat reminiscent of callus tissue in culture (Figs. 5 and 6).

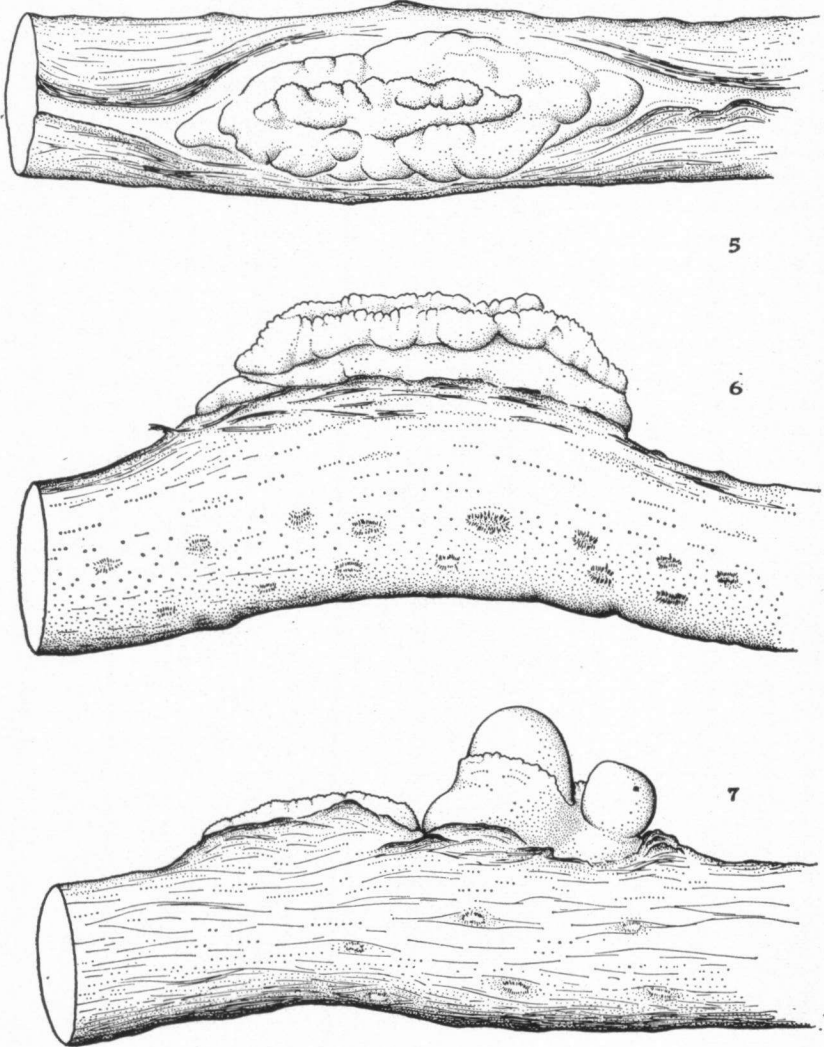
One such haustorium throws some interesting light on the morphological nature of the haustorium in general. Out of the central region of this haustorium (Fig. 7) a pair of typical lateral roots have emerged. The larger of these two quite clearly has the crenate collar of an earlier haustorial crest around its base. It can thus already be seen that there are some deep-seated similarities between roots and haustoria.

The stele of the root, as seen in transection, appears to have "opened out" in the region of the haustorium (Fig. 2). The core of the root at this point is largely parenchymatous. The root itself is not otherwise modified except at the side of the haustorium.

To a student of Santalalean haustoria the lack of external differentiation of the *Phthirusa* haustorium is perhaps the most striking feature. The haustorium is not a separate entity connected to the mother root by a neck, but is merely a swollen portion of it (Fig. 14). Similarly, nothing is visible which could conceivably be called a mantle. Nevertheless, the haustorial organ must be described in terms of a number of successive parenchymatous shells, mutually separated by collapsed cell layers, together surrounding the parenchymatous core known in the literature as "nucleus". (The use of "nucleus" in this context is an unfortunate one, "core" being used in its stead in this paper). The successive collapsed layers are by no means always distinct, and may run from one to the next in what in section appears as a dendritic pattern. Surrounding the parenchymatous core a layer of parenchyma, staining a peculiar purple color when safranin and fast green are used, is a dominating feature. This layer is in the shape of an inverted funnel or flask, and is probably the next collapsed layer; in fact, it is sometimes in a partly collapsed state.

It appears that in the haustorial organs of *Phthirusa* other types of collapsed zones are present in addition to the one discussed above. It is at present not clear to what extent the several types are related. Even the intrusive organ, when entering the host, seems to have a collapsed layer surrounding its axis. A layer of crushed cells has also been noted in a transverse position just behind the attachment surface of young haustoria. It is conceivable that the former is an extension of the latter achieved when the endogenous sucker emerged and passed into the host.

Several young haustoria inspected had, in addition, a more internal, small transverse layer of collapsed cells. This layer is a thin layer but stands out through its separation of two different parenchymatous areas. Towards the host surface parenchyma cells are greatly elongated in the direction of entry, and divide in a transverse fashion only. On



Figs. 5-7. *Phthirusa pyrifolia*, University Greenhouses, Vancouver.

5. Top view of free secondary haustorium. ($\times 20$)

6. Side view of same. ($\times 20$)

7. Side view of one (or two?) free secondary haustoria, the part on the right having produced two endogenous lateral roots from the center of the haustorium. ($\times 20$)

the root-side of this transverse zone cells are isodiametric and have the appearance of meristematic cells. This organization may bear a relationship to the developments leading to host entry, as discussed below.

Within the haustorial organ a number of groups of sclereids are present. They are absent from the root proper; it is difficult to see, however, what connection they may have to haustorial action. Most commonly they are found in a peripheral position just outside the successive collapsed zones. Sclereids seem to be of common occurrence in larger haustoria of *Loranthaceae*. They are very conspicuous, for example, in the haustoria of *Psittacanthus* (KUIJT, 1964a), *Struthanthus* (HEIL, 1926), *Loranthus* (SCHÖNLAND, 1907) and *Antidaphne*.

The vascular supply of the haustorium takes its origin from the root stele which, at this point, is medullated. A definite number of bundles leading to the haustorium does not appear to be present; neither is their course subject to much regularity. The parenchymatous cells forming the matrix around this earliest haustorial xylem are obviously meristematic in nature. It is, therefore, open to question whether we can speak of vascular strands at all in this region. Some haustoria seem to reflect the medullated condition of the mother root, but others appear to have an irregular protostelic xylem system. About all that can be said is that an axial vascular system is present in the young haustorium reaching to the base (i.e., the proximal side) of the parenchymatous core. There seems to have been a rather abrupt halt in the progress of xylem differentiation at this point in many instances. No provascular strands lead into the core. The orientation of vessel members here is perpendicular to the ones directly above, giving the appearance of a terminal pad of xylem. It is possible that such a haustorial "stele" may serve as a brace resisting the pressures emanating from the emerging and elongating haustorial crests. The small collapsed zone mentioned above might be the result of this compression.

Haustorial xylem is not restricted to an axial system in all cases. Individual thin strands of tracheary elements have been seen entering into parenchyma sheaths between recent collapsed layers, but these strands never reach very far. Similarly, the sucker entering host tissues sometimes has peripheral xylem strands quite separate from the axial xylem. The only other known mistletoe with similar "extrastelar" bundles is *Dendrophthoe* (SINGH, 1954).

The nature of the lignified xylem corresponds to that of many other known Santalalean haustoria. Haustorial xylem as described especially by RAO (1942) for *Santalaceae* consists exclusively of vessel members with simple perforations. (The haustorial "tracheids" of *Struthanthus* (HEIL, 1926), *Tupeia* (SMART, 1952), and *Geocaulon* (MOSS, 1926) are here accepted as misinterpretations.) The vessel members are short, with heavy secondary walls in reticulate or scalariform patterns, the perforations frequently appearing on oblique or even side walls. Although quite variable, the vessel members in appearance and size are similar to haustorial xylem elements of *Gaiadendron* (KUIJT, 1965, Fig. 5).

Aside from the main adhesive force supplied by the entire root, adhesion of the young secondary haustorium of *Phthirusa* to the host surface seems to be effected by a columnar tissue, several cells in thickness in the center of the adhesive pad but thinning outwards. These cells are extremely narrow and stain very densely, making precise observations difficult. The haustorial surface molds itself to the contours of the host with the utmost precision. In the case of haustoria on the lower surface of *Nerium* leaves this precision is particularly impressive, as even the host's stomatal crypts are invaded and completely filled by haustorial cells. Neither the flat surface of the young haustorium nor the lobes in stomatal crypts appear to be digestive as the adjacent host cells are of a completely normal appearance. Even the epidermal hairs typical of the crypts are enfolded rather than displaced, and remain alive. There is no suggestion of host entry in relation to the crypts.

We come now to the events leading to host entry. Serial sections of haustoria in the process of entry show clearly that, as has already been anticipated on the basis of external appearance, the intrusive organ (sucker) is endogenous in origin. It is a crest-shaped organ, thin at the margin, which takes its origin from a portion of the core. The first indications of this process are seen in the deterioration of a group of cells in the foremost region of the core, followed by their complete disintegration. The meristematic cells just behind this lysigenous cavity now press forward both by means of longitudinal expansion and cell division, to fill the cavity and break the superficial layer of the haustorium. A successful haustorial crest will then presumably continue its path of advance into the adjacent host tissue. If such entry is not achieved it may be supposed that the crest flattens itself against the host surface, once more producing a functional cementing layer. Such lateral expansion is consistent with the appearance of the haustorium in sectional view (Fig. 4) and may, additionally, be a mechanism to split the host surface (cf. THODAY, 1951).

It should be emphasized at this point that a "gland" as described from Santalaceous haustoria (RAO, 1942) and also known to occur in the mistletoe *Atkinsonia* (MENZIES & MACKEE, 1959) is not recognizable. Its equivalence with the lysigenous cavities of *Phthirusa* and *Phrygilanthus heterophyllus* (REICHE, 1907) is an open question. If this cavity in the latter mistletoes is a modified gland, it is very greatly modified indeed: there is no distinct, specialized cell layer which breaks down, and there is no duct or canal which opens up to the haustorial surface. The final emergence of the haustorial crest is an actual penetration by an endogenous wedge through the superficial layer.

There is, in the literature of Santalalean haustoria, mention of a unique cell type said to combine characteristics of both sieve elements and tracheary elements: the phloeotracheids. First described by BENSON (1910) in *Exocarpos*, "they afford an example of the combination of the structure and function of phloem and xylem elements". The peculiar granularity of these cells reminds one of certain cells described

earlier by HEINRICHER (1895, 1901) from the haustoria of *Lathraea* and *Rhinantheae*. It is perhaps significant that even FINERAN (1963a) in his detailed work on the haustorium of *Exocarпус* is not at all clear as to the structure of the supposed phloeotracheids, and finds them very difficult to observe. It is also clear that, while Benson regarded all haustorial vascular elements as phloeotracheids, Fineran restricts this term to a relatively small core of cells, and regards most haustorial xylem as vessel members. He puts little faith in Benson's suggestion of functional duality of phloeotracheids. His suggestion that they might be active in establishing an O.P. gradient "facilitating a more active uptake of host xylem products" seems premature, however, especially since such a gradient would involve only the entry of water into the haustorium. Unfortunately, no adequate illustrations of phloeotracheids have been produced. Those of BENSON (1910) may equally well be interpreted as differentiating tracheary elements. Even photographs in FINERAN's (1963a) detailed paper are not convincing. Moss (1926) failed to locate phloeotracheids in *Geocaulon* haustoria.

In the haustorium of *Phthirusa* no such cells have been observed, although differentiating vessel members may be found in all regions of the haustorial axis at various times. In fact, in agreement with most earlier work on Santalalean haustoria, nothing remotely resembling phloem was observed. Provascular strands or cambium-like strands are encountered here and there, but are flanked only by parenchyma or vessel members or both. Even if the purple-staining, granular tissue surrounding the core of *Phthirusa* and *Antidaphne* corresponds in position to the phloeotracheids of other species, there are no structural similarities.

Unfortunately my material at present does not allow a description of older haustoria, as it would involve the sacrifice of valuable living material. The haustoria on leaves can scarcely be representative in their endophytic features. The thrust which in these cases carries a haustorial sucker quite through a *Nerium* leaf is normally probably arrested or deflected by the xylem of an attacked stem. From the behaviour of earlier haustorial crests it may be postulated that the tip of the sucker will expand tangentially to some degree. The sequence of events may be parallel for that described below for *Antidaphne*.

In *Phthirusa* the host bark near older haustoria frequently splits (Fig. 15), and entire sections may be lifted up. A considerable amount of lateral expansion seems therefore indicated, although probably not to the extent of that described by HEIL (1926) for some Mexican *Struthanthus*. Such endophytic expansion seems to be predominantly in a tangential, transverse direction with regard to the host branch, if the amount of the shape of local hypertrophy is concomitant with the shape of the haustorium.

The host appears to have little defence against *Phthirusa* attack. An increased mitotic activity has been noted in nearby parenchyma of infected *Nerium* leaves, seemingly forming a protective layer against the haustorium. In general, a single individual of *Phthirusa* does not appear to interfere significantly in host activities when growing on

larger branches. *Codiaeum* branches of about 1 cm in diameter for example, are able to flower in a modest fashion even though a mistletoe is located at the base of the branch. In one case a *Tibouchina* branch died distally to the *Phthirusa* plant, the latter surviving only because of a successful root connecting it to the host trunk. Similar rescue operations were described and illustrated in my previous article (Куйт, 1964) for *Struthanthus* and *Oryctanthus*.

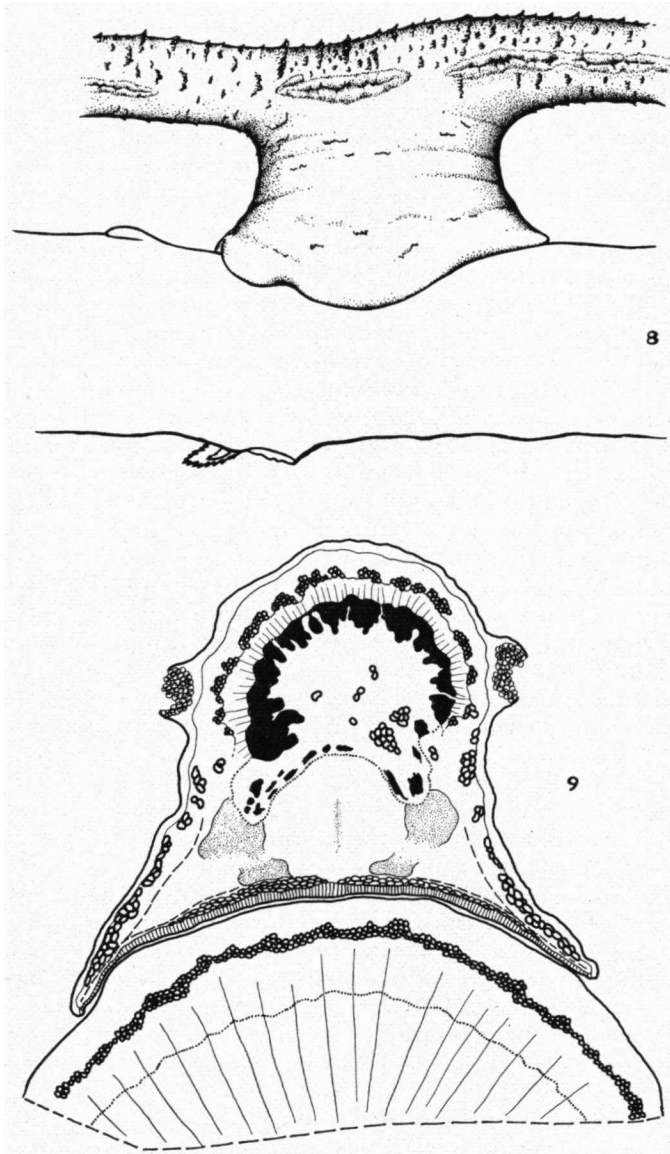
ANTIDAPHNE VISCOIDEA

In the account which follows it is assumed that the primary and secondary haustoria of *Antidaphne* are essentially similar in organization and action. This similarity may not, in fact, apply to all details. Material for an adequate comparative study is not available, however; furthermore, no significant differences are evident in the available material. It will be indicated wherever possible whether the discussion refers to primary or secondary haustoria.

The epicortical roots of *Antidaphne* are of more or less the same proportions as those of *Phthirusa*. They are flatter, however, winding themselves around and extending along host branches as small, brown, scaly ribbons with light margins. Frequently the root tip is not just flattened but even somewhat concave on the ventral side, the root thus being kidneyshaped in transection, even if no host contact is evident. Also, the roots of *Antidaphne* do not achieve the length of those of *Phthirusa*. This difference, as pointed out elsewhere (Куйт, 1964a), is due to a unique feature in *Antidaphne*: its epicortical roots are evanescent, dying back from the apex in older plants. Plants of advanced age have no epicortical roots whatsoever. The primary haustorial connection expands greatly, incorporating in its final shape a number of the nearest secondary haustoria and interconnecting portions of epicortical roots. Such included haustoria may still be faintly recognizable in the lobes of the mature compound haustorium. In contrast to the roots of *Phthirusa*, those of *Antidaphne* are not closely appressed to the host surface. The very apex of the root often does have some physical contact, but the haustoria just behind the apex soon lift the entire root away from the host surface. There is no evidence of a cementing function of the *Antidaphne* root itself.

The light-colored seam, such a distinctive feature of the *Antidaphne* root, is a line of confluent lenticels (Figs. 8 and 9). This compound lenticel experiences an interruption wherever a haustorium is formed. Normally a new lenticel is formed distal to the haustorium, but eventually continuity is established across the haustorial region.

The haustoria of *Antidaphne* are exceedingly discrete structures. Even young ones are large, 2-4 mm in diameter, but older ones may easily reach 20 mm when near the primary haustorium. The appearance of discreteness of young haustoria is due to a well-developed constricted area (neck) and to the formation of a single, wide, flaring mantle which closely fits around one side of the host branch. The free



Figs. 8-9. *Antidaphne viscoidea* on ? *Ocotea* sp., near Tres Rios, Costa Rica. .

8. Side view of secondary haustorium. ($\times 10$)

9. Transection of secondary haustorium prior to penetration. Xylem of parasite in black; collapsed layers in broken lines; cambium in stippled lines; cells in heavy outline sclerenchyma; stippled area surrounding parenchymatous core represents dark-staining tissue discussed in text. ($\times 25$)

surface of the haustorium is smooth and of a mahogany brown color, becoming lighter towards the margins. (A similarly discrete haustorium is illustrated for an unidentified mistletoe in GOEBEL (1932). Fig. 1576.)

The apparent simplicity of the *Antidaphne* haustorium hides a complexity of internal organization not known from any other member of the *Loranthaceae* or even *Santalaceae*. For the description which follows the reader is referred to Figs. 10-20.

The *Antidaphne* root, at the point of haustorial development, has a very large parenchymatous pith with some scattered sclereids, often in groups. In addition to the sclereids, there are groups of lignified elements which are perhaps identifiable as remnants of metaxylem development. The matrix of parenchyma is a very dark-staining tissue, with rather large intercellular spaces. The pith in general is reminiscent of the medullated pith of *Gleichenia* as illustrated by FOSTER and GIFFORD (1959, Figs. 13-14A). The limits of the stele cannot be drawn on the haustorial side, especially since an endodermis is nowhere visible. It is possible, however, to follow the position of the vascular cambium with some degree of certainty. If the line of obviously meristematic cells is followed from the undoubted cambium of the root it is found that the cambium reaches about halfway around the parenchymatous central core. In other words, it rests on the core as an inverted cup. That this layer is indeed the cambium is indicated by the many vessel members forming irregular strands, many cross-connected, above this layer. These vessel members are part of the haustorial xylem as indicated by structural characteristics and staining qualities. They seem to accept less safranin than those of the root. Most of that xylem portion seems to be parenchymatous, and a distinction from the pith is thus impossible. No phloem is formed towards the outside, or indeed anywhere in the haustorium.

The large, central core of parenchymatous cells (to be discussed again below) is surrounded by a massive shell of tissue which, with the usual safranin-fast green staining procedure, becomes a dark purple. In very young haustoria it contains great amounts of starch. It appears to be a modified parenchyma tissue full of very irregular, stain-absorbing granules. A similar layer was described in the above account of *Phthirusa pyrifolia*, where a possible relation to the youngest collapsed layer was noted. No shell-like collapsed layers have been noted around the *Antidaphne* core. It is, nevertheless, possible that this modified parenchyma resists lateral pressure emanating from the core. In many *Antidaphne* haustoria this layer seems to be interrupted by a transverse layer of parenchyma continuous with the core, and extending into the mantle.

The free flanks of the haustorium are covered with a thin corky layer. The cork is supported by an irregular layer of sclereids which are approximately in the shape of the surrounding parenchyma cells. Their heavy secondary walls are interrupted by a striking pattern of wide pits. Interior to the sclereid layer the most conspicuous collapsed layer of the *Antidaphne* haustorium occurs. It begins in the far extremity

of the mantle, reaching up to approximately the neck of the haustorium, where it fades out.

The contact layers of the haustorium are made up of highly differentiated tissues. The superficial layer consists of small columnar cells which are exceedingly narrow, and possess rather dense protoplasm. Consequently these cells are difficult to observe in detail. The layer almost surely is glandular in nature: not only is this function indicated by its structure, but also there is no other method by means of which attachment could be affected. Furthermore, a dark-staining amorphous material is present between the host and parasite surfaces, encasing even individual epidermal cells of the host; this material almost certainly represents an adhesive secreted by the columnar cells. The columnar layer is followed by a layer of lignified cells. This layer is compact and interlocks tightly with the columnar layer below. Its cells are not ordinary sclereids as they maintain living protoplasts. The cells of both columnar and sclerenchyma layers are very rich in tannin. The lignified walls of the latter are relatively thin and perforated by large, circular, simple pits. The sclerenchyma forms a discoid body which nearly spans the entire width of the contact surface. Interestingly enough, the very center of the sclerenchyma disc is interrupted. Immediately behind the sclereids the second collapsed zone is visible, confluent with the above-mentioned one in the distal parts of the haustorial flanks. I cannot be certain from the available preparations that the transverse collapsed zone is present in the axial region.

There remains to be discussed the parenchymatous core of the haustorium, presumably the seat of the intrusive mechanism. The core, unfortunately, seems to experience a great deal of shrinkage during the usual procedures of microtechnique. The young haustoria studied showed a rupture or deterioration of core parenchyma just above the sclereid aperture. The possibility that such a rupture, and the resultant cavity, are a regular event in haustorial development cannot be ignored, but the fact that ruptures appear in other places around the core in other material indicates the former possibility.

In young secondary haustoria the dense-staining shell around the basal part of the core seems to be extended to form a continuous dome above it. In other words, the parenchyma within the dome-like xylem body which is partly differentiated into vessel members, now develops the same, coarse granularity and stain affinities as the adjacent cells. The cambium at its lowest extent retains its normal characteristics and appears, therefore, as a transverse interruption of the dense-staining shell, but it disappears from sight in the inner region of the dome. As in the haustorium of *Phthirusa*, nothing comparable to phloetracheids has been discovered in *Antidaphne*. It is interesting, however, that a very slender strand of vessel members is sometimes present near the periphery of the core well below the cambium, thus indicating a future course of haustorial vascularization. It is also perhaps significant that in young haustoria this same shellshaped tissue contains a great deal of starch which disappears in older haustoria.

The haustorial core itself consists of parenchyma only. The arrange-

ment of cells indicates an active division in predominantly one plane in the young haustorium, resulting in a lateral expansion of the core. The evidence for such a development lies in the plate-like, or file-like outward seriation of parenchyma cells perpendicular to the haustorial axis (Fig. 17) reminiscent of the rib meristems of some shoot apices, and also in the greater size of the cores of older haustoria. The resultant tiered affect is not present in the outer region of the core.

In the young haustorium the central tissue of the core consists of excessively narrow columnar parenchyma cells with very dense cytoplasm arranged in two or more plates. The nuclei are very attenuated and have a large number of heteropycnotic bodies. These extraordinary cells face one another in two layers, each of which is one or two cells thick. By means of transitional cells the two columnar layers grade imperceptibly into the rest of the core parenchyma, but they are delimited from one another by an exceedingly distinct evacuated median plane (Fig. 18). No median canal or duct has been seen.

The mechanism of haustorial entry into the host, in all probability, emanates from the median columnar layer, as interpreted below. My material, unfortunately, does not present a continuous series, and only the following developments can be charted. A gradual deterioration of the cells of the median plate takes place. Starting with the uppermost cells, and in a symmetrical fashion, the cytoplasm of the innermost median cells deteriorates, nuclei become disorganized, and eventually a complete breakdown of cellular contents occurs (Fig. 18). The whole process within each cell appears as a withdrawal of the cytoplasm away from the median plane, leaving a more or less clear space. That this space is not a continuous canal, at least initially, is obvious from the many cell walls still in place. In other words, there is not an early duct between living cells which withdraw from one another. Only the cells adjacent to the median plane are involved in this process, although a later extension to nearby columnar parenchyma is a possibility. This gradual deterioration, which appears to be an autolytic process, proceeds towards the contact surface.

What happens when the surface is reached remains unknown. The materials liberated through the opening of the gland are presumed to be digestive, aiding in the penetration of the columnar layer, and preparing the subjacent host tissues by a softening or a partial dissolution of cell walls. It is possible that the parenchymatous cells alongside the median autolytic layers produce the intrusive organ, possibly aided by the expansion of the cells of the lateral rib meristem. This would involve a reorientation of the tiered layers in such a way that their most median portions would dip down towards the host, the consequent elongation of its component cells being the main force propelling parasitic cells into the host. Such a change in tissue orientation is not only conceivable as it follows the only available escape route from the pressures developed in the core, but is also in accordance with tissue alignments seen in the core region after entry has been achieved (cf. Barber's papers). At such a time all cells in the core region are elongated in the direction of the aperture.

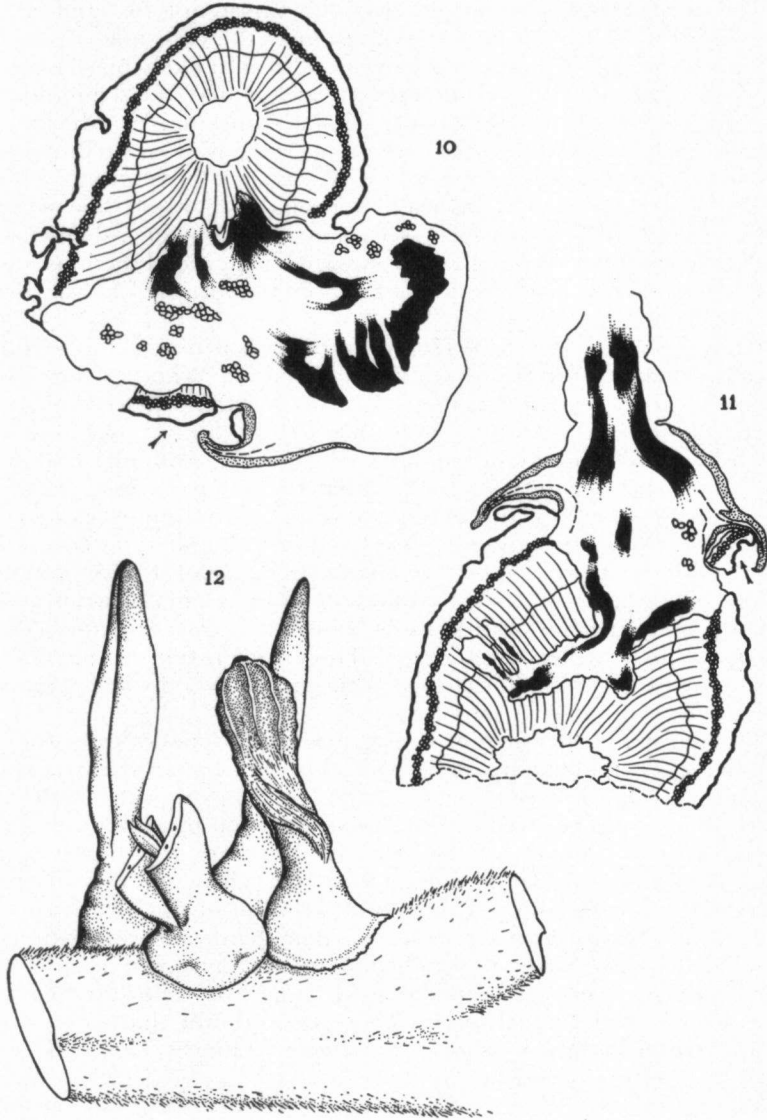
The mechanical aspects of host-entry must not be ignored. The pressures set up by the lateral expansion of the core may result in an actual rupture of the haustorial surface. The most likely place for such a slit to develop would be in the median area, where the sclereid layer is interrupted. These lateral forces will be translated to adjacent host tissues because of haustorial adhesion, and may contribute to an opening up of the host tissues.

The actual process of invasion is probably a rapid one which is, furthermore, hidden from view (see remarks under General Discussion). My material, regrettably, has not yielded such crucial sections, and we must pass on to an account of the endophytic portions of older haustoria.

It appears that the intrusive organ of both primary and secondary haustoria penetrates rapidly to the host xylem. Whether the xylem is entered cannot be said, but the central part of the primary haustorium often is a keel—or inverted cone—like organ (Fig. 11; see also KUIJT, 1964a, Fig. 9e). The main tendency of the young endophyte, however, appears to be tangential growth along the xylem surface, separating the host phloem from the xylem along the cambium. Although some cambial cells are undoubtedly destroyed in the process, an active cambial layer persists external to the anchor-like part of the endophyte and produces secondary tissues, both phloem and xylem. It seems clear, in general, that the host cambium is unusually active in the vicinity of the haustorium (Figs. 10 and 11). The exaggeration of this tendency eventually leads to the formation of the simple wood rose of *Antidaphne* described in my earlier paper.

The flanges of the anchor, connected to the remainder of the plant by means of a much constricted neck (Fig. 11), have the extraordinary capacity to produce centrifugal shafts which grow well into the host phloem, possibly via wood rays. It has not been possible to determine the longitudinal extent of these shafts. They are not, however, mere peg-like organs, but are plate-like in shape. Through their centrifugal growth they bring about a degree of isolation of the host tissues thus embraced which eventually leads to their death and separation from other host tissues. Stages in this development can be seen in Figs. 10 and 11, where patches of eliminated host tissues are still attached to the free surface of the haustorium. There is no doubt that in this rather crude fashion lateral haustorial expansion achieves a greater contact with the vascular tissues of the host.

Little regularity has been discerned in the vascular pattern of *Antidaphne* haustoria. The (sometimes slightly buckled) vascular strands reaching down from the periphery of the haustorial core pass into the "cortex" of the intrusive organ and from then on become highly irregular. The fact that the haustorial axis is not vasculated at the time of entry is often still reflected in older haustoria, as in Fig. 11. Large masses of vessel members interspersed with parenchyma reach to the very base of the haustorium. Rather surprisingly, xylem-to-xylem continuity appears a rather incidental event. Although such contacts are not infrequent, most contact between the two organisms is by



Figs. 10-12. *Antidaphne viscoidea* on? *Ocotea* sp., near Tres Rios, Costa Rica. Primary haustoria of different ages.

10. Older haustorium in transection of host branch. Haustorial xylem in black. Note eliminated host tissues (arrow). ($\times 15$)
11. Similar, but younger. Note centrifugal processes of endophyte, and eliminated host tissues (arrow). ($\times 15$)
12. Four mistletoe seedlings, deposited together by a bird. The seedling with cut leaves is *Oryctanthus occidentalis*, the others *Antidaphne*. Note the pronounced mantle of the latter. ($\times 12$)

means of haustorial parenchyma. Vascularization extends into the centrifugal shafts but, interestingly enough, does not occur in the outer portions corresponding to the adjacent host phloem. It is as if the position of the host cambium dictates the outer limits of haustorial vascularization. It is possible that, as in *Struthanthus* (HEIL, 1926, p. 49), there is a degree of continuity between the cambia of host and parasite.

Anatomically the *Antidaphne* haustorium is thus made up of a matrix of parenchyma, with interspersed groups of sclereids, and permeated by an irregular network of bundles of vessel members. Sieve tube members are not differentiated although they are present in great numbers in the shoot and epicortical root.

It should be mentioned, finally, that no reasons for the evanescent nature of secondary haustoria have been discovered in their structural peculiarities.

GENERAL DISCUSSION

The task before us is to integrate the above descriptions with the existing knowledge of Santalalean haustoria. It should be clear that many primary haustoria of *Loranthaceae*, especially elsewhere in *Viscoideae*, are highly derived absorptive organs which cannot be expected to elucidate the structure and action of secondary haustoria to any extent. The architecture of secondary haustoria elsewhere in the *Santalales* is more directly relevant.

It should be pointed out, nevertheless, that the early development of the primary haustorium of *Antidaphne* parallels the older haustorial systems of several other mistletoes. The same separation of the host xylem from the phloem, the continued activity of the host cambium, and also the formation of centrifugal shafts reaching into the host phloem, have been reported from the genus *Korthalsella* (THODAY, 1958) (*Viscoideae*), and from the *Loranthoideae* *Moquinia rubra*, *Tapinanthus prunifolius*, and others (THODAY 1960, 1961). In some *Santalaceae* the host cambium is similarly raised and may persist in its normal activity (RAO, 1942) as in other *Loranthaceae* where no shafts are formed, e.g. *Loranthus micranthus* Hook. f. (MENZIES, 1954). In the first-mentioned mistletoe genera, shafts may occur in rather large numbers, and may be slender processes or may be knob-like. In all cases, however, centrifugal growth seems to stop when the host phloem is reached. There is no evidence in Thoday's work that the forcible elimination of host tissues as seen in *Antidaphne* also occurs in the above-mentioned genera. In *Korthalsella* parasitism, especially, "separated" host xylem shows no great deterioration and seems to remain functional.

The behavior and structure of older haustoria has scarcely been explored in this study or in others. An indication of the importance of such later developments is seen in Heil's work on *Struthanthus*. This genus develops, from the cortical portions of the endophyte, remarkable, brush-like processes of greatly elongated parenchyma cells which appear to penetrate the host xylem and reach into the host pith. The mechanism of progress, to all appearances, is a digestive one. How

common such sinker-like processes are in mature haustoria of other *Loranthoideae*, and to what extent they are comparable to the sinkers of many *Viscoideae* or even those of *Exocarpus* (FINERAN, 1963b), are questions in need of study.

The discussion should perhaps first focus on the question: What is the morphological nature of the Santalalean haustorium? The literature on the subject presents some rather divergent views on this question. One of the basic criteria in this regard has, in the past, been whether or not the haustorium is exogenous or endogenous. Even on this simple question there is considerable disagreement. We find, for example, that HEIL (1926) claim endogeny for both epicortical roots and haustoria in *Struthanthus* (*Loranthaceae*). It is not surprising that this author reaches the conclusion that haustoria are modified roots. In fact, he goes one step further and compares lateral endophytic lobes with lateral roots of a higher order, surely a comparison bereft of all meaning.

Equally defensible, and equally incomplete, is the notion that secondary haustoria are exogenous. After all, there is not, around the base of the haustorium, the rim of cortical and epidermal tissue which identifies a lateral root as an endogenous organ. Thus we find that RAO (1942) in his survey of the Santalaceous haustorium states categorically that the latter is exogenous. MENZIES and McKEE (1959) are of the same opinion for *Atkinsonia* (*Loranthaceae*), and others could be added who are of the same opinion. No one seems to have gone so far, fortunately, as to declare the secondary haustorium stem-like because of its exogenous origin!

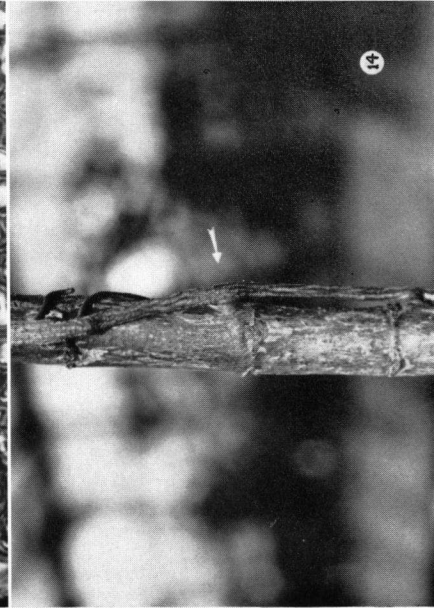
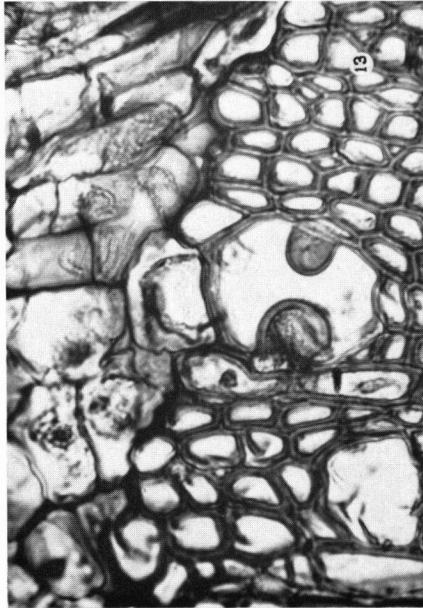
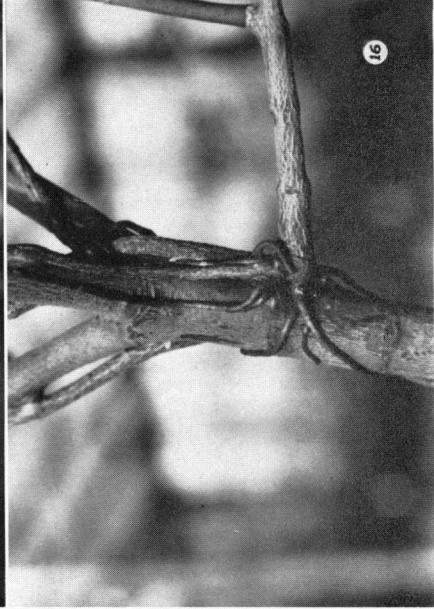
I would first like to point out the fallacy inherent in the criterion endogeny vs. exogeny when used in isolation of other facts. The primary shoot of some *Orobanchaceae* is also endogenous (KADRY and TEWFIC, 1956) but there is no question as to its morphological nature; the same is true for the primary shoot of *Lennoa* (SUESSENGUTH, 1927), and for the inflorescences of *Balanophoraceae* and flowers of *Rafflesiaceae* (see, for example, UMIKER, 1920). In other words, the endogenous development of an organ is not in itself a diagnostic fact with regard to morphological identity.

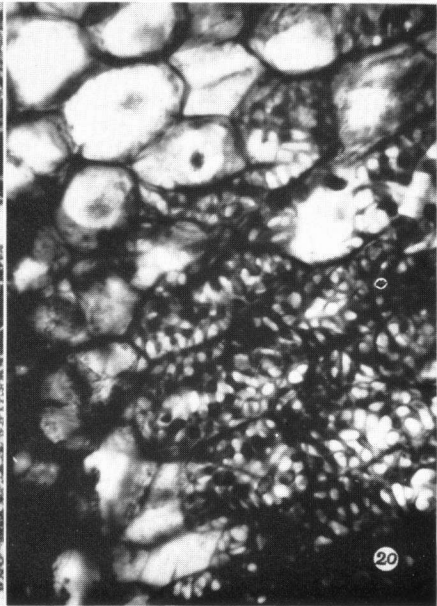
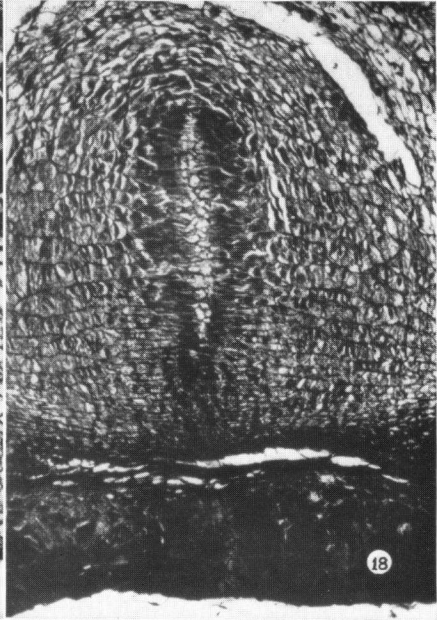
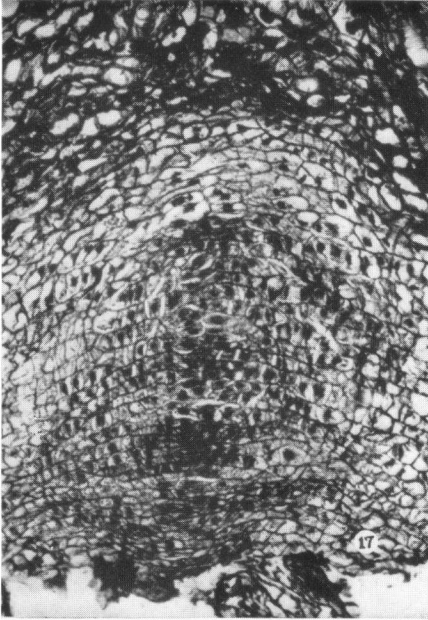
The fact is that the Santalalean haustorium is neither wholly endogenous nor wholly exogenous. It is rather surprising that a larger number of authors has not reached the same conclusion, as this fact is

Figs. 13-16

13. Two tyloses formed in vessel member of host near haustorial parenchyma of *Antidaphne viscoidea* (above.) (Ca. \times 750)
14. *Phthirusa pyrifolia* on *Nerium oleander*. Epicortical root and secondary haustorium (arrow) of ca. 18 months in age.
15. *P. pyrifolia* on *Codiaeum variegatum*. Three primary haustoria (arrows), showing splitting host bark and numerous epicortical roots. Plants ca. 2 years old.
16. *P. pyrifolia* on *Nerium oleander*. Primary haustorium and numerous epicortical roots.

J. KUIJT: *On the Nature and Action of the Santalalean Haustorium, as Exemplified by Phthirusa and Antidaphne (Loranthaceae)*





easily ascertained. Surely no one can take issue with the statement that the peripheral tissues of the haustorium, including all of the mantle, are derived from extra-stelar root tissues? At the same time, there is nothing in the literature which denies the endogenous birth of the intrusive organ, the organ which actually invades the host. The present work on *Phthirusa* and *Antidaphne* once more has established quite clearly the penetration of the haustorial surface layers by an intrusive organ which is of internal derivation. If we are to regard the Santalalean haustorium as an entity, therefore, we must concede that it is partly exogenous and partly endogenous. There is no real basis for a controversy here. It is unfortunate that more recent authors have failed to consider similar conclusions elsewhere in the literature on *Santalaceae* (MOSS, 1926, for *Geocaulon*; BARBER, 1906, for *Santalum*; SABLON, 1887, for *Thesium* and related genera; BARBER, 1907*b*, 1908, for *Olex* and *Cansjera*).

The arrangement of the xylem within the haustorium has also been given considerable weight in morphological interpretation. To provide a clear example, SINGH (1954) declares the primary haustorium of *Dendrophthoe falcata* to be stem-like in nature because of its siphonostelic anatomy. Presumably this argument would be equally applicable to secondary haustoria of a similar construction, although this corollary seems not to have been expressed. A look at the architecture of the epicortical roots of *Phthirusa*, *Antidaphne*, *Struthanthus* (GOEBEL 1932; HEIL, 1926), *Phrygilanthus heterophyllus* (REICHE, 1907), *Loranthus micranthus* (MENZIES, 1954) and indeed of *Dendrophthoe falcata* itself (THODAY, 1960, footnote p. 143) takes away the basis of Singh's argument, for epicortical roots themselves are clearly medullated at least at the site of haustorial insertion. The same can be said for the roots of some terrestrial Santalacean genera; BARBER (1907*b*), for example, states that there is little difference between this region of the root and the stem of *Santalum album*. The vascular system of the haustorium, therefore, is not conclusive as to its morphological identity.

In all considerations, variation is of considerable importance. Surely, it would be most unreasonable to assign the haustoria of related Santalalean parasites to different morphological categories merely on the basis of somewhat different origins and vasculature.

Figs. 17-20. *Antidaphne viscoidea*, details of secondary haustoria.

17. Transsection of parenchymatous core, showing "rib meristem" and early appearance of median gland. Some vessel members are present in upper left and right corners. (Ca. \times 125)
18. Transsection of older stage with median gland extending down in direction of contact surface (black) and the host (out of view). Zones of rupture around and below core due to faulty microtechnique. (Ca. \times 200)
19. Transsection of intrusive organ (sucker). Host phloem has been penetrated, but the intrusive organ has been diverted by host xylem (lower right). Note collapsed layers extending from the core to the advanced regions of the endophyte. (Ca. \times 45)
20. Reticulate haustorial vessel members, seen in somewhat oblique section of the haustorial flanks. (Ca. \times 500)

The fact is that even with regard to the origin of the intrusive organ within these haustoria a blanket statement cannot be made. In some species it seems derived solely from the haustorial core (*Olaix scandens* and *Buckleya quadriala*; SOLMS-LAUBACH, 1867-'8, and KUSANO, 1902). But in others its tissues spring partly from the core, partly from the haustorial cortex (*Santalum*, *Osyris*, *Thesium*; see BARBER, 1907c) which, in turn, is a derivative of extrastelar root tissues. With regard to stelar structure, a siphonostelic arrangement prevails, but at least two interesting exceptions exist: the secondary haustoria of *Olaix scandens* (BARBER, o.c.) and *Exocarpus* (FINERAN 1963a), and the primary one of *Viscum album* (THODAY, 1951) are essentially protostelic (at least with respect to the intrusive organ), lacking pith, and developing a single median plate of xylem. Young *Gaiadendron* haustoria are connected to the mother root only by two vascular strands (KUIJT, 1965). Such variations show the need to bear in mind the ontogenetic and evolutionary plasticity of haustorial organs. It is unlikely that such vitally important organs as Santalalean haustoria, adapted to such a wide range of host plants, should be conservative organs. Morphological concepts based upon them are clearly more secure when embracing them all.

Within the above context there seems, in the last analysis, little reason to deny Santalalean haustoria an affinity with roots. Once again a careful consideration of facts would seem to return the same judgment which an unbiased layman instinctively makes, namely that haustoria are modified roots. Such a superficial evaluation is based on the obvious actions of haustoria: absorption and anchorage. A somewhat more informed botanist tends to be overwhelmed by a series of unorthodox departures from his traditional concepts of the root. Yet, if we think of a haustorium as a highly modified lateral root, in which the apex makes a rather delayed appearance, and which is assisted (and to some degree preceded) by the coordinated growth of the cortex of the mother root, then no concrete objections remain to this concept. The Santalalean haustorium is a root in function and in evolutionary origin. It may be of interest, at this point, to refer to parasitism in *Lennoaceae* (KUIJT, 1966). In that family, parasitism is undoubtedly of more recent origin than that in *Santalales*. In *Lennoaceae* a root dimorphism has evolved, resulting in large, coarse roots and minute haustorial roots. It is not inconceivable that the Santalalean haustorium is an evolutionary elaboration of a lateral root similar to the haustorial root of *Lennoaceae*. (It is an interesting fact that BARBER (1906) reports root hairs from *Santalum* haustoria.)

STRUCTURE IN RELATION TO ACTION IN SANTALALEAN HAUSTORIA

There are perhaps more than a thousand parasitic species in the Santalalean complex of families. We should, therefore, anticipate a considerable amount of diversity in the way in which the haustoria operate, and, consequently, in the way they are constructed.

A few remarks are justified, perhaps, at this point on the symmetry

of Santalalean haustoria. The impression of radial symmetry so often given is false and, as pointed out by THODAY (1951), a result of sections is only one plane. Even if the haustorial shape is radially symmetrical, as is frequently true of primary haustoria of *Loranthaceae*, the internal organization is bilaterally symmetrical. It is natural that the anatomy of secondary haustoria, which spring from roots in all cases, should reflect in some way the direction of the mother root. This is obvious in *Phthirusa* where the intrusive organ is a wedge-like organ the plane of which passes through the mother root's axis, unaffected by any possible curvature of the host stem. In *Gaiadendron*, however, quite the opposite appears to be true: the orientation of the wedge seems to be dictated by host contours. Fig. 15 in KUIJT (1965) shows a case where the roots of host and parasite are more or less perpendicular to one another, the intrusive wedge developing parallel to the host root and consequently at a considerable angle to the mother root. Yet, when *Phthirusa* attacks a flat organ (a leaf; see above) the wedge is parallel to the mother root. It would be interesting to know the orientation of the wedge of *Phthirusa* roots which are growing *around* a branch. One obtains the impression of a primary control by host contours which, when neutral, allows the wedge to develop parallel to the mother root. It is also possible, however, that in root parasites a wedge parallel to the host root is the only efficient one, as others might sever the root completely. In parasites on branches (which are always much more massive than roots of comparable age) such a host-control is superfluous, and has perhaps been supplanted by a control through the mother root.

In primary haustoria the situation is inherently different, as the wedge cannot orient itself with respect to the stele of a mother root. That a flat wedge is formed here also is evident from the present work on *Phthirusa* and *Antidaphne*, and also from studies of *Oryctanthus* (KUIJT, 1964a, Fig. 6), *Viscum* (THODAY, 1951), and *Dendrothoë* (SINGH, 1954). Primary haustoria, it should be noted parenthetically, are in *Santalales* known only from *Loranthaceae* and *Myzodendraceae*. Whether or not there is a relation between wedge-orientation and position of cotyledons is an open question. THODAY's (1951) study gives no indication of this possibility, perhaps partly because of the greatly reduced cotyledons in *Viscum*. Yet his work suggests that the orientation of the wedge is not determined by the host surface or host tissues, as he describes wedges which have entered in different positions. After entry, endophytic lobes proceed in the length direction of the host branch and may thus take their origin from the edges, or from the flat side of the wedge, depending upon the latter's position. In *Phthirusa* seedlings grown on a flat piece of glass I have not obtained any clear idea as to the direction of the wedge with respect to the cotyledons. The above discussion does not take into account the frequent lobing of the radicular apex upon contact in *Viscum* (THODAY, 1951), *Phoradendron*, and possibly others. It also cannot go into details about the extreme bilaterality of haustoria of *Ximemia americana* (BARBER 1907c) and *Nuytsia floribunda* (HERBERT, 1919) where two opposing mantle lobes grow in opposite direction around the host root and meet

on the other side. In *Nuytsia*, fusion of the two lobes is said to occur, forming a noose-like ring from the inside of which intrusive processes invade the captured root.

The nature of the action which allows entry into the host has been speculated upon by nearly every worker in the field. Recent workers seem to allow for both a mechanical action and the participation of enzymes. That there can be no doubt as to the former is amply demonstrated by the dislocation and physical disruption of considerable amounts of host tissues, as seen in sectioned material. The action by means of enzymes has not been unequivocally demonstrated. The discoloration and breakdown of host tissues in contact with the haustorial organ, or any substances present between living tissues of host and parasite, are in no sense a secure indication of chemical action. Possibly the only convincing evidence of chemical action by the haustorial organ is the discoloration of adjacent host tissues where no penetration has as yet occurred. Such distant action was noted in the case of the *Santalum album* haustorium by Barber (1907a, p. 42), host xylem, parenchyma and sclerenchyma being affected before any disruption occurred. A similar case has been noted just below the median region of *Antidaphne* haustoria. The evidence of penetration of cork by *Viscum album* seedlings (THODAY, 1951) is again no proof of chemical action.

The question of chemical action by Santalalean haustoria is intimately connected with the existence and interpretation of the gland. One of the main difficulties in the study of this elusive tissue is its capricious appearance: even in a single individual some haustoria are with, others without a gland (BARBER, 1906). There are persistent references in the literature to the relation between the development of a gland and the kind of root attacked. Thus, haustoria of *Santalum album* attached to roots with much sclerenchyma are said to develop a distinct gland (BARBER, 1906), and a similar situation prevails in *Osyris arborea* (RAO, 1942). Nevertheless, BARBER (1906) seems to be justified in stating that the presence or absence of a gland cannot be predicted in any given case. Since glands appear prior to penetration it is difficult to see how the haustorium "senses" the degree of hardness of a healthy root, unless a biochemical specificity to root exudates is involved.

The actual structure and development of the Santalalean gland are again known only in vague outline. Aside from the complexities encountered by BARBER (1907b) in *Olax*, the gland is elliptical or fusiform in sectional outline, and of a bilateral symmetry. The constituent, transversely elongated cells always seem to experience a centrifugal deterioration and withdrawal of cytoplasm. Whether this process always leads to a breakdown of the evacuated portions is an open question. In *Santalum* (BARBER, 1906) and *Geocaulon* (MOSS, 1926) a more or less schizogenous cavity eventually results, but the gland in *Olax* is said to be lysigenous (BARBER, 1907b), as comparable areas in *Atkinsonia* (MENZIES and MCKEE, 1959), *Dendrophthoe* (SINGH, 1954), *Exocarpus* (FINERAN, 1963a), and *Phthirusa*. A preformed

duct is said to be present in *Cansjera* (BARBER, 1908), implying a schizogenous separation of cells.

It might also be rewarding to take a fresh look at the various collapsed layers met in Santalalean haustoria. The presence of at least one collapsed layer—running parallel to the sides of the haustorium, in the outer cortical region—seems to be a nearly diagnostic feature of haustoria in the *Santalales*. The only two possible exceptions to this rule known to me might be the genus *Nuytsia* (HERBERT, 1919) and the extremely advanced genus *Arceuthobium*. In neither case, however, has an adequate account been produced of the crucial stages. Nothing comparable to collapsed layers is known to me from other parasitic families. It has been generally assumed that collapsed layers are caused by pressures originating elsewhere, in the haustorium.

THODAY'S (1951) suggestion that the collapsed layers are actually *contractile* layers, similar to those in many contractile roots, gives the question of haustorial action an entirely different complexion. This would mean, if true, that the collapsed layers, far from being crushed by expanding tissues in the axial regions, actively contribute towards haustorial penetration. It is certainly possible that the lateral and transverse collapsed layers in *Antidaphne*, for example, have such a function. Their collapse, or contraction, might add considerable purchase to the intrusive organ, the haustorial margin being held in place by the adhesive substance produced by epidermal cells. Thoday cites some observations on *Viscum album* which would substantiate such an upward pull of part of the haustorial contact surface.

My observations on germination of *Phthirusa* are in agreement with the latter suggestion. *Phthirusa* seeds, when kept moist, germinate rapidly on glass plates. The haustorial disk which forms on the surface of the glass can thus be studied from below, through the glass. The disk, representing the transformed radicular apex, rapidly assumes a circular outline. This seems to be accomplished by rapid growth in the area of contact and not, as THODAY (1951) reports for *Viscum album*, in areas of the disk furthest from contact. The circular haustorial "face" is flat and closely appressed to the glass at first. Almost immediately the green center, lengthening into a green line, announces the formation of an haustorial wedge. It is soon after this that a separation takes place from the glass in a ring-like zone halfway between the margin and the developing wedge. It is possible that this observable withdrawal is due to the vain efforts of the wedge to penetrate the glass and thus is not related to the collapsed layers. It is perhaps more likely, however, that the withdrawal is caused by a contracting layer, thus adding thrust to the intrusive organ. Since the outer collapsed layer normally extends far into the haustorial margin (*Cansjera* being somewhat of an exception: BARBER, 1908), contraction there might result in a stronger grasp on the host root. In fact, even the subdermal sclerenchyma layer in *Cansjera* and *Antidaphne* might in this way be ascribed a function, namely the lessening of local collapse of the haustorial flanks, thus transferring the entire effect of contraction to the contact surface. It would seem unlikely, however, that the same

explanation would apply to the collapsed layers of the *Phthirusa*-type of haustorium.

The collapsed layers in endophytic parts as presented for *Antidaphne* (Fig. 19), *Phthirusa* (Fig. 2), *Loranthus micranthus* (MENZIES, 1954), and *Santalum* (BARBER, 1907a) may similarly be explicable as tangible evidence of longitudinal contraction of intrusive organs. The fact that, in most of these cases, the direction of contraction is perpendicular to that of the presumptive contractile layer does not militate against Thoday's suggestion. The same is true for the contractile roots of *Oxalis incarnata* (THODAY, 1926), where the transverse contractile parenchyma layers show a remarkable similarity to the Santalalean collapsed layers. The fact that, in *Oxalis incarnata*, contraction is an effect of water deficit may also have some relevance in haustoria.

Another mystery is represented by the dark-staining layers just outside the haustorial core. We have seen such a shell-like layer nearly surrounding the core in *Antidaphne*, where the tissue contains much starch when young; and we have seen them associated with collapsing layers in *Phthirusa*. In *Viscum album*, THODAY reports a collapsed layer just outside a starch-laden shell of parenchyma surrounding the core. A more dome-like starch layer rests on the haustorial core of *Olax* (BARBER, 1907b), where some starch-filled cells also become part of the collapsed layer. Another comparable instance is present in haustoria of *Struthanthus* (HEIL, 1926). A somewhat different starchy layer is present in *Cansjera* (BARBER, 1908). As *Olax* haustoria, following host entry, have exhausted their starch supply it seems reasonable to suppose that this starch is utilized in the process of invasion.

It is possible that the upper area of dark-staining cells corresponds to what has been reported as the *interrupted zone* in Barber's work, and as phloeotracheids by BENSON (1910), and recently by FINERAN (1963a). The reader is referred to the above discussion of *Phthirusa* for phloeotracheids. The interrupted zone as described by Barber for *Santalum* and *Cansjera* is an apparent interruption of the xylem connection between haustorium and mother root where a progressive, centrifugal deterioration and reabsorption of secondary walls of vessel members is said to take place. Cell lumina become filled with gummy substances. This deterioration is said to be a very rapid development. It is perhaps significant that the interrupted zone could not be located by RAO (1942) and other workers, although the thoroughness of Barber's work makes one hesitate to condemn this aspect of his studies. Barber himself was quite baffled by the interrupted zone and could not provide an adequate explanation of it.

It seems, therefore, that a study of the literature, or a casual study of one or more selected species cannot elucidate the vascular transition between the haustorium and the mother root. Whether phloeotracheids, darkstaining, collapsed, and starch-containing layers are all developmental phases of the same tissues, or whether in this regard we are again confronted with differences of a taxonomic nature, cannot be decided at present. Only more careful work, focussed particularly on the transition region, can lead to a clarification.

Virtually none of the descriptions of the gland in *Loranthaceae* and *Santalaceae* leave the reader with a clear idea as to the exact origin of the intrusive organ. The impression is usually left that the latter is either a tubular organ, or a reconstituted solid organ after the gland has been obliterated and reabsorbed. We see, on the one hand, illustrations of the remnants of glands having been bodily pushed out into host tissues (BARBER, 1907a, 1908). On the other hand, Moss (1926) figures a gland in *Geocaulon* which has been bypassed on all sides by xylem strands uniting distally. This version thus involves a fusion of the apical tissues surrounding the glandular duct into a single intrusive organ, the sucker. RAO (1942) simply speaks of replacement of the gland by other tissues, leaving the question of the origin of the sucker open. In *Phthirusa* and *Phrygilanthus heterophyllus*, discussed above, the sucker originates above an internal cavity (possibly comparable to the gland in other species), grows through it and the superficial tissues to reach the host. Once more, in summary, we obtain glimpses of a diversity in structure some of which will surely be of a taxonomic nature, others representing ontogenetic differences, or being caused by inadequate materials.

One of the chief difficulties in the study of the gland and of the events surrounding host entry is the great rapidity with which the latter seems to be accomplished. At least in highly differentiated haustoria, all signs point to a slow build-up, and elaborate preparation, followed by a sudden entry into the host. Such a rapidity would explain the difficulty in finding haustoria which are in the process of entering. Not only my own work on *Gaiadendron*, *Antidaphne* and *Phthirusa* suffers in this regard; in fact, only Barber has come near to capturing the crucial moment of entry. Even he, nevertheless, complains of the same difficulty; of 130 *Olex* haustoria inspected by him, none were in the act of penetration! As Barber says, a great and sudden elongation of all the cells of the core probably coincides with the formation of a split in the host bark. Several of Barber's illustrations show the changes in orientation and shape of cells of the core as a result of this surge; the organization of the *Antidaphne* core (above) has been interpreted similarly. It scarcely needs emphasis that this process may not have a parallel in some other Santalalean haustoria such as *Exocarpus* and *Phthirusa*.

Compound haustoria, i.e., haustoria showing more than one mantle, or showing a series of superimposed cores, are known from a number of genera. They are thought to be a response to host roots which are particularly difficult to penetrate, and for this reason may occur in many more species than known at present. The following list of known instances may not be complete: *Osyris arborea*, *Thesium wightianum* (RAO, 1942), *Santalum*, *Opilia*, *Cansjera* (BARBER, 1907c), *Geocaulon* (Moss, 1926), *Gaiadendron* (KUIJT, 1965).

Compound haustoria seem to be consistently absent in *Olex* (BARBER, 1907c) and *Antidaphne*. It would seem, however, that intermediate situations exist. In *Phthirusa* one obtains the impression of a greatly telescoped and simplified compound haustorium the mantles of which

are only weakly developed. A nearly identical type of haustorium seems to exist in *Loranthus micranthus* (MENZIES, 1954) where bursts of growth, each represented by a new, endogenous meristem, succeed one another. (From Menzies' illustrations it appears that the young epicortical roots in this mistletoe adhere closely to the host and have inconspicuously mantled haustoria, as in *Phthirusa* and *Struthanthus*, thus providing an interesting parallel.)

HOST ANATOMY NEAR THE CONTACT ZONE

While some facets of host response to invasion by mistletoes were touched upon in an earlier account (KUIJT, 1964a), the scope of the present work requires some additional comments.

The anatomy of the xylem-to-xylem contact may first be briefly considered. In a number of articles a rather precise conformity of pitting along the contact zone is referred to. It must be admitted, however, that adequate illustrations are lacking of this phenomenon, which would have great physiological significance. From surveying the literature, in fact, one receives an impression of indiscriminateness in the termination of haustorial xylem. Barber's work quite clearly leads to the conclusion that, while the general tendency certainly is towards a xylem-to-xylem contact, haustorial vessels do not discriminate between fibers, vessels, parenchyma, and rays of the host. SOLMS-LAUBACH earlier (1877) had reached a similar conclusion. If a precise correspondence of pitting of tracheal elements of host and parasite is found it might thus be a chance occurrence. Selfparasitic haustoria of *Ola*x, and possibly in *Scleropyrum* (RAO, 1942), result in a precise fusion of the comparable tissues of the two systems, but this is perhaps more properly regarded as a graft-union. In the parasitism of *Antidaphne* as reported above, the xylary contact is again characterized by irregularity.

In several instances a wound reaction involving the formation of tyloses and the deposition of unidentified, dark-staining materials has been noted in host xylem. Both of these phenomena were described by Barber in his various papers on *Santalum*, *Ola*x and *Cansjera*. In some of the hosts attacked by these parasites, the tyloses extending into their vessel members developed a secondary wall with reticulate pitting reminiscent of haustorial vessels. It may thus be surmised that, when MOSS (1926) and MENZIES and MCKEE (1959) speak of, and illustrate the penetration of a vessel member by an haustorial element, they might indeed have been concerned with tyloses slit open by the microtome knife.

While it is true that the deposition of gum and the differentiation of tyloses even to the extent of secondary wall deposition are apparently normal phenomena in certain woody species (ESAU, 1965), the distribution of gummy materials and tyloses in attacked roots and branches convincingly establishes both phenomena as pathological responses. In the species studied by Barber, tyloses and gummy materials were

virtually restricted to host tissues in close proximity of haustorial tissues. The same is true for the host branches parasitized by *Antidaphne*; tyloses of this sort are represented in Fig. 13. Such observations agree closely with those of ESAU (1948, p. 427) who found similar phenomena associated with virus diseases of the grape vine and peach.

SUMMARY

1. The young haustorial organs of *Antidaphne* are exceedingly discrete and anatomically complex organs, with various parenchyma, sclerenchyma and other tissues, but provided with only a single mantle. Most interesting is a definite glandular structure in the median region, a tissue not heretofore reported from epiphytic *Loranthaceae*. The precise origin of the intrusive organ is not known. The endophyte is unusual in that its tangentially expanded lobes produce centrifugal processes out to the host cortex, thus isolating patches of host tissues.

2. The secondary haustoria of *Phthirusa*, in contrast to those of *Antidaphne*, are very inconspicuous because of a virtual lack of mantle, and the entire root adheres to the host surface. A series of endogenous processes are produced, each one from the inner tissues of the previous one and each one attempting to enter the host. A recognizable gland has not been found, but the lysigenous cavity formed just in front of each endogenous wedge may be comparable to the gland of other parasites.

3. Epicortical roots in *Loranthaceae* are true roots, as indicated by their root caps and endogenous origin, even though a pith is present. The primary roots of all epiphytic mistletoes lack root caps and are provided with a single tunica.

4. The Santalalean haustorium is partly exogenous, partly endogenous in development. It is believed to be an evolutionary derivative of a root.

5. In *Loranthaceae* with epicortical roots two types may be recognized:

- (a) roots when young adhering closely to host, the ventral layers of the root and haustoria sharing the function of adherence: greatly reduced mantles; repeated succession of endogenous processes leading to host invasion; poorly differentiated glandular cavity.
- (b) only the haustoria in contact with the host, their ventral columnar, glandular layer being highly differentiated; a single prominent mantle (i.e., simple haustoria); well differentiated gland; invasion accomplished by a single thrust rather than by repeated efforts.

To what extent this distinction is valid among the other Santalalean families is not known.

6. Young primary and secondary haustoria are presumed fundamentally the same in action and organization, with the exception of their vascular connection to older tissues and organs.

7. The intrusive processes (suckers) of Santalalean primary and secondary haustoria are not peg-like in shape, but rather like flat wedges. The mechanism determining the orientation of a wedge is not known, but apparent instances of internal control and control by the contours of the host are cited.

8. The occurrence and significance of collapsed layers in Santalalean haustoria are discussed. Some of these layers may, in fact, be contractile layers. Collapsed layers are characteristic of Santalalean haustoria.

9. The Santalalean gland is a puzzling tissue of erratic occurrence. Its function is presumed to be the production of digestive substances in connection with host entry, but this has not been convincingly demonstrated. There is some evidence to the effect that the nature of the host organ attacked may determine whether or not a gland is produced.

10. An elusive tissue or cell type is represented by the phloetracheids, reported from the haustorial neck of some species. No trace of such a tissue has been encounter-

ed in *Phthirusa*, *Antidaphne*, and many others. Another puzzling tissue is a shell-like parenchymatous, dark-staining tissue associated in various ways with the parenchymatous core.

11. Haustorial xylem in *Santalales* consists of reticulate-pitted vessel members in a matrix of parenchyma. Discrete strands are rarely recognizable, and both siphonostelic and protostelic arrangements are known.

12. Phloem as a differentiated tissue is absent in Santalalean haustoria (except for one recorded case of self-parasitism in *Olex*), the vascular contact being exclusively xylary. Nevertheless, a close conformity in pitting has not developed, the terminal haustorial vessel members scarcely discriminating between various host tissues.

13. Host tissues frequently respond to the presence of haustorial lobes by an excessive production of tannins, by the extrusion of gum-like substances into tracheal elements, or by the formation of tyloses.

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